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PROBLEMS OF BIRD-MIGRATION

PROBLEMS OF BIRD-MIGRATION

BY

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TO

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IN SOME ACKNOWLEDGEMENT OF THE INFLUENCE WHICH
HIS TEACHING ON THE BIOLOGICAL PROBLEMS
CONCERNED HAS HAD ON THESE ORNITHO-
LOGICAL STUDIES OF HIS SON, FORMER
STUDENT AND SOMETIME
ASSISTANT

"To be sufficiently qualified for this task, it is necessary that the inquirer should confine himself to one certain tract the whole year; he should be particularly careful to mark the exact period of the arrival and disappearance of birds; he should observe in what order the different species come, and at what time, and in what manner they go; also how they steer their course, whether east, west, north or south; he should commit every observation to paper, and compare them with the remarks of others who have written on the subject; he should likewise attend to the temperament of the air, and to the plenty or failure of fruits and berries, as on these accidents many curious and advantageous remarks may be made; he should cultivate an acquaintance with the gentlemen of the navy, consult their journals to discover what birds alight on the ships, and at the same time should endeavour to learn at what seasons they appeared, in what latitude, etc. Were these methods vigorously and strenuously pursued, we might easily trace them to their respective abodes."

"A NATURALIST" [John Legge]. *A Discourse on the Emigration of British Birds.* London, 1795. (First edition, Salisbury, 1780.)

PREFACE

THIS book aims at a statement of the problems presented by the phenomenon of bird-migration, rather than at an attempt, hopeless in the present state of knowledge, at their solution. These problems have a wide importance from the point of view of biological theory, migration in birds providing one of the most remarkable examples of animal behaviour: at the same time they are of great interest to all observers and lovers of nature to whom the facts which they concern come each year as an undiminished wonder. The subject, fortunately, is one which can be discussed in a scientific manner without technicality, and the writer has thought it practicable to attempt to keep both groups of possible readers in view: on the one hand the biologists who may wish to have a presentation of the essential facts; and on the other hand the ornithologists and bird-lovers who may wish some account of the theoretical aspects. It results, of course, that to some who fall in one group or the other, and especially to those who may be placed in both, some parts of the book must inevitably seem elementary.

In order that the special problem of avian migration may be seen in its true perspective, there is given, by way of introduction, a brief review of the migratory phenomena found in the Animal Kingdom as a whole. Following this, the main substance of the book falls naturally into three parts. Firstly, there is an outline of the principal known facts. Secondly, there are some more detailed studies by way of illustrative example. Thirdly, there is the statement and discussion of the main theoretical problems.

In the first two chapters of the second part of this book there is given, by way of introduction to the studies which follow, some account of observational methods on the one hand and of the marking method on the other. From these it will be gathered that very much research in the subject has been done in the last thirty years or so, all adding to our knowledge. It is surprising, therefore, that within this

period—that is, since the publication of Dixon's *The Migration of Birds* (1892, 1897)—no book dealing with the subject in a general way seems to have appeared in this country, except Mr. T. A. Coward's very short, although useful, *Migration of Birds* (1912). The subject has, of course, received a chapter in various books of wider scope, such as Mr. W. P. Pycraft's *A History of Birds* (1910) and Professor J. Arthur Thomson's *The Biology of Birds* (1923). There are also general chapters, and an unrivalled summary of migration in the British area, in Dr. Eagle Clarke's *Studies of Bird-Migration* (1912), a work, however, which in the main fulfils the different albeit more important function of presenting its author's own contributions to the subject. The present writer has therefore ventured to believe that a book of the kind here presented is not unneeded.

In dealing with such an extensive subject the writer has of necessity aimed at generalisation and example rather than at completeness of detail. Of the essential facts anything more than a summary outline was obviously impossible in view of the vast quantity of data available in the scattered literature of the subject. For more detailed consideration, too, only selected examples could be dealt with, and these from a restricted point of view. The writer thinks, however, that he need make no great apology for the stress which he has laid, especially in the second part of the book, upon the results of the marking method : not only is this method responsible for the most recent additions to our knowledge, not to be found in earlier works, but it represents the line of study in which the writer has himself been most closely engaged and about which he may therefore most fittingly speak. It is, nevertheless, fully recognised that the greater part of our existing knowledge is based on the results of older methods, themselves by no means obsolete, and that the new study is but beginning to extend an already wide horizon.

It may be added that there are few countries so well situated as the British Isles in geographical relation to the phenomena of migration, and no country where more attention has been paid to the scientific study of the subject. Little excuse is therefore needed for drawing the facts employed in the present work mainly from north-western Europe and especially from the British Isles. In theoretical matters the attempt is made, however, to keep the treatment as wide as possible.

ACKNOWLEDGEMENTS

The writer's opportunities for making original investigations in the subject have been largely due to the fact that for several years, from 1909 onwards, he was able to conduct an inquiry by the marking method from the University of Aberdeen. His thanks are due in this regard to the Carnegie Trustees for a grant towards the cost of the work, to the numerous co-operators who helped to increase the scale on which the marking was done, and to all those who kindly reported the recovery of marked birds. The inquiry came to an end during the war, in the writer's absence, some co-operators continuing longer than others while their stocks of rings lasted. The practically complete results were subsequently published in the *Ibis* in 1921, and a selection of them has been utilised in the second part of this book.

After the conclusion of the Aberdeen University inquiry, the writer was able to assist to some extent in the work of the remaining large-scale inquiry in this country, that associated with *British Birds*. He is greatly indebted to Mr. H. F. Witherby, editor of that magazine, for invitations to work out parts of the results of the inquiry, combining them for the purpose with the Aberdeen University records and with such foreign data as were available from published sources. The conclusions, in part embodied in this book, have already formed the subject of papers in *British Birds*, during the preparation of which the writer was indebted to Mr. Witherby for much helpful advice as well as for the provision of part of the data. This inquiry, happily, still continues in active being, and it is destined, as further results accumulate, to add in important ways to our knowledge of the subject.

To the respective editors of the *Ibis*, the *Scottish Naturalist* and *Nature*, as well as of *British Birds*, the writer makes acknowledgement of the re-use of the substance of papers which he has already published in these periodicals.

In other respects, as is necessarily the case with a book of this kind, the writer is much indebted to the work of others, both predecessor and contemporary. Due acknowledgement of this fact is made at the relevant points in the text, except in dealing with what may be regarded as matters of general knowledge, and in the lists of authorities at the ends of most of the chapters: it need scarcely be

said that in the great majority of cases these authorities, with very many others, have been consulted in the original.

The writer's chief acknowledgement, however, he has already made on the dedication page of this book.

Finally, throughout the preparation of the work the writer has been greatly assisted by his wife. Since its completion he has also become further indebted to Mr. H. F. Witherby for helpful criticisms of the manuscript as well as for arrangements for publication.

A. L. T.

LONDON, *1st December*, 1925.

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PROBLEMS OF BIRD-MIGRATION

INTRODUCTION

MIGRATORY MOVEMENTS IN THE ANIMAL KINGDOM

" The locusts have no king, yet go they forth all of them by bands."
PROVERBS, XXX, 27.

Power of free movement characteristic of animals—Movements other than migratory—Changes in nature of habitat without change of locality—Definition of true migratory movement—Migratory movements among crustaceans—Among insects—Among fishes—Among reptiles—Among mammals—Among birds—General survey—Periodicity and rhythm—Cyclical phenomena—Orientation and " Homing " —Hibernation as an alternative to migration.

To obtain a true biological perspective for this book's particular subject of bird-migration it seems desirable to begin with a review, necessarily in no more than brief outline, of the subject of migratory movements in the Animal Kingdom as a whole.

The power of free movement from place to place is, with some exceptions on both sides, characteristic of animals as distinguished from vegetable forms of life. Even the proverbial limpet moves over the surface of the rock to which it clings ; even the sedentary sea-anemone can seek new moorings in case of need ; and in organisms like the barnacle and the sea-squirt the fixed adult form is preceded by a free-swimming juvenile stage. In relatively few cases is the power of free movement altogether given up. A few of the lower forms such as sponges are plant-like in habit and remain rooted all their lives to the selfsame spot, perishing if the conditions there become unfavourable. Many parasitic animals, too, are fixed in the sense that they move only with their hosts and are transported passively from one host to another in a way that rather resembles the dispersal of seeds in the Vegetable Kingdom.

Not all movements from place to place deserve to be called migratory, however, even in a wider sense of that term than is used in ornithology. One may, for instance, exclude the circumscribed movements, whether of a few inches or of several miles, which an animal performs in the ordinary course of its daily life—the crawling of the starfish on the floor of the sea or the prowling of some beast of prey in the jungles. One may also rule out all purely fortuitous movements, mere random wanderings in search of food, and all wholly passive movements such as those of pelagic organisms borne by ocean currents or of young spiders sailing on the breeze by means of their threads of gossamer. Further, one may disregard those gradual movements, generation after generation, whereby a race of animals may extend its range as opportunity offers.

In passing, brief reference may be made to those transitions from one kind of habitat to another which occur in the case of many animals which have larval stages very different in structural characters from the adult form. Thus, many different marine animals when fully developed are relatively stationary inhabitants of the littoral zone but have free-swimming larvæ which seek the open water for a time. Similarly, the larvæ of insects may be aquatic or terrestrial, although the corresponding adult forms may be mainly aerial in mode of life ; and in the transition from the water to the land which occurs when a gill-breathing tadpole becomes a lung-breathing frog there is a more drastic change of environment than could be brought about by any mere movement from place to place. Again, there are various kinds of parasitic worms which pass different phases of their life cycles in different kinds of animals : the liver-fluke, for instance, is found as an adult in the bile-ducts of the sheep and in one of its larval stages in a water-snail, while there are intermediate stages when the organism is at one time free-swimming in the water of a pool and is at another quiescently encysted on a blade of grass. These, however, may conveniently be left out of account here because they are changes in the nature of the environment in which movement from place to place—geographical migration—is either practically absent or of only secondary importance.

To deserve the description " migratory," in its strict sense, movements need not necessarily have a very great geographical amplitude, but at the least they must involve a definite change of locality. They must be purposive in

that the change of scene is associated with some definite advantage which serves as its *raison d'être*, and there must be return movements to the original area. They must be periodic in that they correspond to some recurrent change either in the environmental conditions themselves or in the animal's reaction thereto. True migrations are changes of habitat, periodically recurring and alternating in direction, which tend to secure optimum environmental conditions at all times.

Within the scope of this definition one may therefore proceed to a survey of the migratory movements known to occur in the different classes of animals. It is not, however, until the Arthropods are reached, in ascending the scale, that anything is found sufficiently definite to be worthy of special consideration here.

Crustaceans

A definite seasonal migration is known to occur, for instance, in the case of the Edible Crab (*Cancer pagurus*), a common species on the British coasts. According to Pearson, the Crabs leave the tidal shore area in September and move out to where the water is some twenty or thirty fathoms in depth. The return movement begins in February after spawning has taken place, and the fertilised eggs which the females bring with them are hatched in the inshore waters. Williamson connects these movements with the conditions of temperature and food-supply. The shallow waters are the warmer in summer, the period of hatching and development, but the deeper waters have the advantage in winter: nevertheless, the shallow waters are still the warmer of the two when the offshore migration begins in autumn. It is possible that the autumn storms have some influence on the movements.

Meek (1902) has shown that the Crabs are not necessarily merely local in these movements: individuals marked in Northumberland, especially females, have been shown to return from deep water to parts of the coast as much as eighty miles distant. The same writer (1903, 1905) has shown that the Lobsters in the region named are less migratory than the Crabs, and quite local in their sphere of movements: a movement of two miles along the coast in the space of a month was an extreme case for a marked animal.

Interesting migratory movements have been observed in

the case of certain Land-Crabs, these being mainly terrestrial in their habits but remaining dependent on the sea for the purposes of reproduction and early development. On this subject Calman writes as follows : " In the case of *Geocarcinas ruricola*, a species very common in the West Indies, the migration to the sea takes place annually during the rainy season in May. The Crabs are described as coming down from the hills in vast multitudes, clambering over any obstacles in their way, and even invading houses, in their march towards the sea. Stebbing states that ' The noise of their march is compared to the rattling of the armour of a regiment of cuirassiers.' The females enter the sea to wash off the eggs which they carry attached to their abdominal appendages, or rather, probably, to allow the young to hatch out. The Crabs then return whence they came, and are followed later by the young, which, having passed through their larval stages in the sea, leave the water, and are found in thousands clinging to the rocks on the shore." Similar habits are found among the terrestrial Hermit-Crabs, as, for instance, in the case of the " Robber-Crab " or " Coconut-Crab " (*Birgus latro*), a very large species which dispenses with the usual portable shelter and has the habit of climbing trees.

Insects

Regular migrations, in accordance with the strict definition adopted here, do not seem to occur among insects, and it must be remembered that the span of life of the winged adult is usually very short. Nevertheless, mention must be made of the concerted mass movements on a large scale which take place in some cases, and of which the Locusts provide the classical example.

Locusts of various species are found in different parts of the world, some of them having a very wide distribution even apart from the temporary extensions of range which often result from the emigratory movements. These movements are made by the insects in dense swarms, and consist of sustained flights in definite directions which possibly depend upon the direction of the wind prevailing at the time. The extraordinary destruction of vegetation which follows the arrival of a swarm in a new region is only too well known to the inhabitants of the affected countries. Movements, naturally of much less extent, are also made at times by the wingless young.

According to Uvaroff want of food in the original area is not the cause of the movements of Locusts, as a region of plentiful food supply may be left. Temperature, he considers, is the governing factor. Very little, however, seems to be accurately known about the periodicity of the migrations. The extent of single flights, at least on occasion, may be judged from the fact that swarms have been encountered on the Atlantic Ocean 1200 miles from land.

In many parts of the world, too, great flocks of Butterflies may be observed from time to time flying steadily in a constant direction, and these have even been met with out at sea. During the voyage of the *Beagle*, when the ship was off the east coast of South America, this came to the notice of Charles Darwin, who wrote of it as follows : " One evening, when we were about 10 miles from the Bay of San Blas, vast numbers of Butterflies in bands or flocks of countless myriads, extended as far as the eye could range. Even by the aid of a telescope it was not possible to see the space free from Butterflies. The seamen cried out that 'it was snowing Butterflies,' and such in fact was the appearance."

Hudson gave this description of a great movement witnessed by him on the pampas of South America : " The red *Vanessa* Butterflies travelled close to the surface, singly or in twos or threes together, passing at intervals of a second or two, so that it was easy to count them as they flew by. On the occasion of the second migration I marked a space of a few feet, staked at the sides, and counted all those passing over it in an hour, and calculated that 65,000 Butterflies had passed over every hundred yards during the flight, which lasted from nine o'clock in the morning to a little after five in the afternoon. The breadth of the migration column was about three miles. On the following day they continued for about seven to eight hours passing in the same numbers, then the numbers began to decline, and on the third day the whole migration finished. During the whole time of my watching, the Butterflies kept always so close to the surface as to be almost touching the grass, travelling always at the same swift rate of speed, and never did I see one alight to rest."

Similarly, Beebe describes how vast numbers of *Catopsilia* Butterflies perform movements in Guiana with a general north-north-westerly direction. The course of the great rivers seems to be followed, and the flights observed

consisted wholly of males. The same writer has also seen flights far off the coast proceeding out to sea in the same direction.

The foregoing instances have been quoted because of the impression which they give of movements of Butterflies actually in progress, but there are many references in entomological literature to the quasi-migratory habits of various species in different parts of the world. From summaries of some of the chief instances given by Poulton and by Williams, it would appear that no general rule can be laid down. Sometimes the movements occur at irregular intervals and in other cases they seem to be regularly annual. Insects of both sexes may take part ; but on many occasions the travelling swarms have been found to consist entirely or largely of one sex, commonly the male, a fact which has not been satisfactorily explained. A rapid rate of flight and fixity of direction are characteristic. In many cases the movements are in one direction only, apparently representing a great exodus from an area which has probably become overcrowded relatively to the available food-supply, and to which there is no return : in other cases subsequent movements in the reverse direction have been noted. In some but not in all cases the direction of flight is determined by the wind, the relationship differing with the species : regularly alternating winds may thus explain the to and fro movements recorded in certain regions.

A very remarkable point about the migrations of some Butterflies is that there are annually repeated invasions of regions where the species is unable to survive throughout the year : there is no return movement, and the eventual result—one which seems to deprive the migration of any kind of advantage for the race—is the extermination of all the immigrants and their descendants. Thus the Monarch Butterfly (*Danaida plexippus*) does not survive the winter in the temperate parts of North America, but each summer there is a considerable northward movement, which is said to be continued by the next generation later in the season.

There is a good British example of the same thing in the case of the Painted Lady (*Pyrameis cardui*). According to Frohawk, the first immigrants reach this country in May or June, sometimes in enormous swarms, but in some years only in small numbers. They breed if conditions are favourable, and the insects of the next generation emerge as adults in August ; but none survives the winter here.

A particularly large immigration occurred in the autumn of 1903, when hundreds of thousands were recorded on the eastern and southern coasts, from the Shetland Isles to the south of Ireland.

The Red Admiral (*P. atalanta*) is another annual immigrant to the British Isles from the south, although in this case successful hibernation here has been known to occur. Both this and the previous species, it may be remarked, are sometimes recorded as on the wing at night. Migrations of some kind are performed by several other British species, including the Large White (*Pieris brassica*), which is a plague in some years and scarce in others, and the Clouded Yellow (*Colias edusa*), an annual immigrant in varying numbers.

Although many of these movements of Butterflies end in the destruction of the travellers, it is to be noted that in other instances new areas are successfully colonised. A remarkable example of this is provided by the Monarch Butterfly, already mentioned, which has a wide range in the American continents and is well known there for its wandering habits. The species has now become established in the islands of the Pacific Ocean, in Australia, and in New Zealand. It has also extended its range to this side of the Atlantic and has frequently reached the British Isles. Walker is of the opinion that carriage by ships has played no more than a secondary part, and that the spread is largely natural. As in some other instances, colonisation of Hawaii followed the establishment there of the appropriate food-plant.

Movements of swarms of Dragonflies of various kinds have also been described. Felt quotes a case in which large numbers were seen at sea 900 miles from Australia and 300 from the Cocos-Keeling Islands: the latter have apparently no indigenous species, but are frequently visited.

Few or none of these insect movements are true migrations, for there is little evidence of return movements. It may be remarked, however, that short to and fro movements, very regular in their directions and times, have been recorded by Le Prince and Orenstein in the case of *Anopheles* mosquitoes in Panama. The insects bred on flooded land some little distance from Gatun, and regular passage towards the town in the evening and from the town in the morning was observed to take place.

Fishes

Most fishes have great mobility, and in the sea there is ample scope for movement. It is, however, very difficult to observe the movements of marine fishes, and knowledge of the subject is at present very far from complete. Owing to the economic importance of the problem, much attention has of late years been paid, in particular, to the movements of some of the food-fishes of the North Sea, such as, for instance, the Herring (*Clupea harengus*), the Plaice (*Pleuronectes platessa*), and the Hake (*Merlucius merlucius*) : the studies include observations by the method of marking individuals, which will later be considered very fully in the case of birds. The results of this work are contained in a great number of technical reports on particular investigations, and the subject seems still to be in a stage when it is difficult to draw general conclusions. For present purposes it will suffice to state some broad facts.

There are probably three different types of movement to be recognised in the case of many marine fishes. In the first place there is the purely passive drift of the eggs, and perhaps to some extent of the very young fry, determined by the direction of currents and by other physical factors. Then there are the wanderings of the fishes in search of food : these movements may follow a more or less regular seasonal cycle, and lead to great concentrations at particular places at certain times. Finally, there are the spawning migrations. These last lead the fishes to particular localities, or types of locality, for the purposes of reproduction, and they are the movements to which the term " migration " may be most properly applied.

As already stated, it is difficult at present to generalise on the subject. Nevertheless, it seems safe to say that there is at least a common tendency to seek shallower water at the time of spawning. Shallow waters are usually inshore waters, of course, and in some cases the movement extends into the brackish or fresh waters of estuaries and rivers. In the extreme cases the spawning migrations involve long journeys to the higher reaches of the rivers, and of this the Salmon is a familiar example.

The Salmon (*Salmo ferox*), then, shows an alternation between a period of reproduction in fresh water and a nutritive period in salt water. It is in the late summer or in the autumn that the adult fish ascend the rivers, and in

Scottish streams the height of the spawning season, as stated by Calderwood (1907), is in November or in early December, according to locality. The eggs hatch out in the spring, and by the end of the year the " fry " have become " parr," and rather resemble small trout in appearance. It is usually in spring that the " parr " put on the silvery coats of the " smolts," and then go down to the sea. They may revisit the fresh waters as " grilse " in the following year, or they may remain in the sea, feeding and growing, until they are adult salmon, four to six years of age, and then return to the rivers to spawn. The adults do not feed to any appreciable extent in fresh water, and when they return to the sea after breeding it is as lean and poor-conditioned " kelts." Apparently it is common for them to breed only once in their lives : some, indeed, die after spawning, but others recover their condition in the sea and may grow to great size. (In some American species of Salmon, all die after spawning, and there is thus no return to the sea.) There are points in the story as here briefly outlined which are still disputable, possibly owing to individual and local variations in habit leading to conflicting observations, but the main outline is sufficiently clear for present purposes. It may be added that fish marked as " smolts " have been shown to return to the same rivers as " grilse " or as adult salmon : evidence on this point, with regard to Scottish streams in particular, has been given by Calderwood (1922).

Although a common tendency, as has been said, is for spawning migrations to take place from deep waters to shallow, or from salt waters to fresh, for the purposes of reproduction, there are cases in which this does not apply. In some instances there are little or no movements at all, and in others the movements are perhaps indifferent in this respect. In others again, the tendency seems to be reversed : of this the clearest example is to be found in the extraordinary life-history of the Eel.

In the case of the Common Eel (*Anguilla vulgaris*) the nutritive phase is spent in fresh water and reproduction takes place in the sea. As the Danish investigator, Schmidt, has shown, the breeding place of the Eels which visit European rivers is in deep water in the south-western part of the North Atlantic. The developing eggs have not yet been found, but the thin transparent larvæ, or *leptocephali*, rise to the surface, where they live for some time without feeding. Movement towards the coasts of Europe

and North Africa follows, but the journey takes about three years: those bound for the rivers of the eastern Baltic, for instance, have some 3000 miles to go. As they near the coasts they become cylindrical instead of flat in form, and shorter in length. It is in spring that great multitudes of the young Eels, or "elvers," ascend the rivers, and their passage in millions—the "eel-fare"—is a remarkable spectacle: movement is by day. In sluggish reaches of the rivers, and in lakes and ponds—which may be reached, over stretches of damp meadow, even though land-locked—there follows a long period of feeding and growth. There is, however, no breeding in fresh water, and when, after several years, the Eels are full grown, they suddenly begin to undergo great constitutional changes and to become silvery in appearance. Then, commonly in autumn, they at last return to the sea, travelling down the rivers mainly by night. Their goal is the waters of the North Atlantic, where they were born and where they are now about to breed: apparently reproduction is followed by death, for none ever returns. The breeding grounds of the American species, *A. rostrata*, overlap those of the Common Eel; these American Eels have thus a shorter distance to go to reach the rivers of eastern North America, and it is interesting to note that with this shorter journey is correlated a shorter period of development.

It is not proposed to discuss here the various theories that have been advanced as to the factors which determine the movements of fishes. Such things as the temperature and salinity of the water, the set of currents, the changes in the abundance and distribution of food supply, are among the possible external agents. Account has also to be taken of internal physiological stimuli, arising, it may be, from the stage of development, the state of nutrition, or the ripening of the reproductive organs. One general fact of great importance may be noted: the whole answer cannot lie in the external forces. The Eel, for example, behaves differently in the several stages of its life-cycle. External conditions probably play a part, because a seasonal element is apparent, but the same conditions do not always provoke the same response. It is not in every or any autumn that an Eel starts down stream for the journey to its oceanic breeding grounds, but only in the year which finds it attaining maturity.

Reptiles

Turtles of various species make periodical journeys from the open water to the land for the purpose of laying eggs in the sand of the sea-shore. The adult Turtles leave the shore when the eggs have been laid in the sand, and when the young hatch out they find their own way unerringly to the sea. In the words of Parker, writing of the Loggerhead Turtle (*Caretta caretta*), "to see a dozen of these newly hatched creatures, that have had no previous experience of the ocean, scramble towards it, notwithstanding that it may not be within the range of their vision, is a sight never to be forgotten." This observer, extending earlier work by Hooker, has made interesting experiments on the subject of their behaviour. In a series of trials under varying conditions, young Turtles were liberated upon a piece of cardboard within a pen having sides about 6 inches high, cutting off the low horizon from their view. The conclusion was that the young reptiles possess a tendency to move down slopes, a tendency to move towards regions in which the horizon is open and clear and away from those in which it is interrupted by complicated masses such as groups of trees, and probably also a tendency to move towards blue areas rather than towards those of other colours. They are not to be appropriately described as phototropic, as they do not move towards or away from a source of light, but exhibit a more complex condition responding to the details of their retinal images rather than to these images as wholes.

It is not known that journeys of any considerable extent are made by the Turtles between their periodical visits to the land. Experiments made by Schmidt, with the Green Turtle (*Chelone midas*), of which he marked a number in the West Indies, gave no evidence of great movement: 50 miles was the maximum distance recorded, the interval in this case being ten months.

A parallel to the behaviour of Turtles in visiting the land is to be found in that of various Sea-snakes, which periodically come inshore to the shallow water for the purposes of reproduction.

Mammals

It is probable that all Arctic mammals migrate to a greater or less extent, and similarly in mountain regions throughout the world there are regular movements from the higher to

the lower levels on the approach of winter. Good examples of regular seasonal migrations are afforded by such animals as the Reindeer in Northern Europe and North America.

Dugmore has described the migrations of the Newfoundland Caribou (*Rangifer terranovæ*), a species of Reindeer, and these will serve as an illustration. There is a regular autumn movement from the storm-vexed mountains of the northern peninsula to the milder regions towards the south coast of the island, and a return movement in spring. The autumn migration sets in after the mating season, usually in the latter part of October. Wintry weather is often the signal for its inception, and the sudden onset of very severe conditions sometimes produces a veritable stampede. More commonly the journey is accomplished at a sharp walking pace. The animals travel for the most part by day and in relatively small companies, walking in single file. At first does, fawns and young stags predominate, most of the big stags coming rather later. The same general route is kept to each year, and in places the same actual track is followed to such an extent that the rock has in the course of years been worn by countless hooves to a depth of 2 or 3 feet.

These movements of the Caribou are not readily explicable. The autumn migration is clearly related to weather conditions, and probably to the covering of the ground moss, on which the animals feed, by snow or a coating of frost. The factors operating in the spring movement, which takes place when the does are heavy with young, are less obvious. Moreover, in both the northern and the southern parts of the island some Caribou remain throughout the year.

On the great plains of Central Asia there are seasonal movements of the vast herds of ungulate mammals; and in South Africa there are likewise well-known "treks" of such animals as the Springbuck, doubtless due to the effect of rainfall, or the lack of it, upon vegetation: with the eaters of grass there may also move attendant carnivores. Exceptional droughts cause great movements from time to time in many tropical and sub-tropical regions.

The migratory movements performed by some species of Bats, the only mammals with powers of true flight, do not appear to be well understood. Bats of more than one species native to the American mainland are not infrequently recorded in the Bermudas, and flocks have also been encountered by ships 20 miles out at sea. According

to Willey, "flying foxes" (fruit-eating Bats) rest during the day among the palms of a certain islet off the coast of Ceylon, going to the mainland to feed by night: in doing so they alternate with flocks of Crows, which roost in the same palms at night and visit the mainland by day.

Among marine animals, the Seals of various kinds have to make periodical visits to the land for the purposes of reproduction. They may come merely from the neighbouring waters, as in the case of the Common Seal (*Phoca vitulina*) of British seas, which is believed to be non-migratory. The various species which breed in the polar regions, however, perform long journeys from the seas in lower latitudes to which they resort for part of the year. Thus the Alaska Fur Seal (*Callorhinus alascanus*) comes as far south as northern California in winter. Nelson states that "in spring they leave the north-west coast and many of them travel steadily across more than 2000 miles of the North Pacific. For days at a time they swim through a roaring gale-swept sea, under dense, low-hanging clouds, and with unerring certainty strike certain passages in the Aleutian Islands, through which they press to their breeding grounds, more than 100 miles beyond, on the small fog-hidden Pribilof Islands."

The movements which are performed by Whales (which are of course wholly aquatic) do not seem to be sufficiently known to permit of generalisation.

In addition to such regular annual movements as have been mentioned, there are less frequent movements, sometimes on a great scale, which take the form of more or less sudden invasions of new territory. The classical example is that of the Lemming (*Lemmus lemmus*), a small rodent well known no farther off than Norway. At intervals of a few years a great increase in numbers is followed by an overflowing of the usual boundaries. This is notably the case in southern Norway, where the Lemming is normally confined to the higher mountain levels, but on these occasions descends to lower ground. Vast numbers of the animals march together in a steady stream over hill and dale, devouring as they go and preyed upon in turn by an attendant escort of birds and beasts of prey. (According to Berg, the Peregrine Falcons which come on the scene prey not on the Lemmings themselves, but on the attendant Short-eared Owls and other birds.) Nothing turns them from the straight line of their course: swift streams are crossed

despite heavy losses, the traffic on roads is no obstacle, and often the procession reaches the sea and heads out towards inevitable destruction. Collett has described a case in which a vessel sailed for a quarter of an hour through water which was alive with swimming Lemmings.

The overcrowding is commonly followed by an outbreak of epidemic disease, and both in the original territory and on the invaded ground the animals are killed off until the population is reduced to a low ebb, and is confined to its normal area. Similar fluctuations in numbers and similar epidemics of disease among the animals occur elsewhere in Lemmings of various species, and, indeed, also among such other animals as Mice and Rabbits. Migrations naturally take place only when there is a possible outlet for the surplus population, as in the case of the Lemming in southern Norway: in northern Norway, for instance, this species is normally found down to sea-level, and there is thus little room for overflow.

According to Elton the "Lemming years" show a regular periodicity with an average interval of 3·6 years, a point to which further reference of a more general kind will be made later on in this chapter. Moreover, the cycle of events in different areas is synchronous. The ordinary distribution of the Lemming in southern Norway consists of isolated areas of high ground, but the exodus from the different mountain blocks takes place in the same season. The allied Wood-Lemming (*Lemmus schisticolor*), living at rather lower levels, appears to increase and migrate in the same years as its relative. In general, "lemming years," irrespective of species, coincide within a year in different parts of the world, so far as the data suffice to show, even in such widely separated regions as Norway and Canada.

Movements of this kind are not true migrations. There is no return journey, and most of the travellers perish. Sometimes, however, new territory is successfully colonised, as in the sudden southward extension of the Elk in Russia, about 1870, which Hilzheimer says was noted by Slitkow. In 1727, according to the same writer, Pallas saw huge crowds of Brown Rats (*Mus decumanus*) crossing the Volga after an earthquake, and this was about the time of the appearance of the species in Europe. More commonly, successful extensions of range are gradual, each increasing generation spreading outwards beyond the zone of its predecessors.

Birds

Here it is necessary to anticipate only in the briefest form the subject matter of the succeeding chapters. Among birds there are very many examples of regular seasonal migrations between a summer breeding-area and a winter area in which milder conditions then prevail. There are also cases in which similar movements of a less regular nature take place under exceptionally severe weather conditions, and changes of level in the case of otherwise stationary birds inhabiting mountain regions. One may further distinguish, perhaps, the probably erratic wanderings of certain sea-fowl, into which a regular migrational element is introduced by the periodical return to the coastal breeding stations. In addition there are certain remarkable exceptional movements, notably those of Pallas's Sandgrouse (*Syrrhaptes paradoxus*), which take place from time to time and appear to constitute a parallel to such phenomena as the exodus of the Lemmings.

General Survey

Among crustaceans, fishes, reptiles, mammals and birds may be found good examples of true migration, that is to say, of regular movements between two alternate habitats. In the most highly developed forms of migration both habitats are definite localities, while in others there may be one definite locality and a wider area of more or less nomadic movement : it is possible that in still other cases movement is between two different kinds of habitat rather than between definite localities.

Among insects, mammals and birds there are also found examples of less regular movements which are of the nature of occasional nomadic enterprises rather than of true migrations, but of which it will nevertheless be desirable to say more in the case of birds in a later chapter.

Any discussion of the particular problems of migration in other animals than birds is beyond the scope of this book, and no more has been aimed at than a brief account of some illustrative examples for purposes of comparison. There are, however, a few general characters of migratory movements to which it may be well to give some preliminary consideration along the broader lines of this chapter, leaving over more detailed discussion of their ornithological aspects to the concluding part of the work.

Periodicity and Rhythm

One of the salient features of a true migratory movement is its regular recurrence, and it may therefore be useful to consider briefly the general question of periodicity in animal life and its particular application to the immediate problem. In various ways the lives of animals are conditioned by periodic changes in the external environment, and of these there are at least three ordinary kinds. The alternation of day and night introduces a periodic element into the lives of many animals, as we well know in our own case. For marine animals inhabiting the littoral zone the ebb and flow of the tides is more important: thus many marine worms and molluscs live at the mouths of their burrows when the tide is in and retire to the bottoms of these when the tide is out. (There is also the fortnightly cycle of tidal maxima, and the alternating spring and neap tides are known to induce a reproductive rhythm in some animals.) Finally, there is the sequence of the seasons, the alternation between summer and winter in the higher latitudes, or, say, of a wet season and a dry season nearer the equator. It is the seasonal periodicity which is of course important with regard to the migrations of animals, for the diurnal and tidal alternations are obviously too frequent to admit of any noteworthy changes of locality adapted to their varying needs and dangers. Of longer periodic cycles, affecting the race rather than the individual, something will be said below.

There are also a few cases of periodicities apparently related to the monthly cycle of lunar phases. That the size of certain marine invertebrates varies with the phases of the moon is a statement frequently found in the literature of classical Greece and Rome and of the Middle Ages—"*Luna alit ostrea et implet echinos*" (Lucilius)—and is a belief which still persists in Mediterranean countries. Munro Fox has recently found it to be untrue of the various Mediterranean species of echinoderms, molluscs and crustaceans which he investigated, but, curiously, true of the large Diadem Urchin (*Centrechinus setosus*) of the Red Sea. In this species spawning takes place at each full moon during the breeding season. Further, the reproductive "swarming" of the Polychæte worms known as "Palolo," notably *Leodice viridis* of the Pacific coral reefs, takes place at the last quarter of the moon in the month or months

of the breeding season. Whether these periodicities are directly related to the amount of moonlight, or are related to the lunar cycle through tidal or other indirect influences, is a point upon which the experimental evidence is as yet inconclusive. One would of course expect a tidal periodicity to be fortnightly, as there are spring tides and neap tides twice in each lunar cycle: "nevertheless," as Fox says of *Centrechinus*, "during the summer months at Suez the new moon spring tides have a greater range than the full moon springs, so that the maximum tidal range is attained once only during each lunar month." (It is probably only to an increased restlessness on bright moonlight nights that Guérin refers when he speaks of a lunar periodicity in the behaviour of certain aquatic birds.)

One must take into account also the periodicities which may arise within the organism itself. Herring has cited physiological evidence of various kinds in favour of his view that "fluctuation," that is the alternation of periods of full activity and complete rest, is a fundamental property of the cell units of many, and possibly of all, living tissues. However this may be, examples of intrinsic rhythm are to be found in the contractions of the vacuoles of Infusorians, in the processes of cell division, in the movements of ciliated epithelium, in the functioning of the vertebrate heart: of longer periodicities there could be no clearer case than that of the cycle of uterine changes in women.

For present purposes the most important periodicity is the commonly found alternation between a nutritive and a reproductive phase. Even where an individual reproduces only once in its life there is yet periodicity in a racial sense. Sometimes this periodicity is purely intrinsic, as in some marine animals which show a regular alternation between reproductive and non-reproductive phases although living in the sea at a depth which ensures almost unchanging conditions of environment. (A parallel case is that of tropical trees which are subject to no seasonal influences and do not show the growth-rings in their wood: they have regular cycles of flowering and fruition, but at any one time different individuals may be found in all stages.) More frequently, however, the physiological periodicity is to some extent governed by or linked with the alternation of the seasons, so that, for instance, summer may be the time of reproduction. In investigating the factors in seasonal migrations, therefore, it is necessary to consider whether the external changes are the more important or whether

the seasonal periodicity of the movements is a secondary aspect consequent on the coincidence of the physiological changes in the animal itself. Point is given to this question by the fact that all seasonal migratory phenomena are not annually recurrent: it is not in every spring that an Eel migrates up-river, but only in the spring which finds it at a certain stage in its development; and similarly it is only when it reaches reproductive age, after having let the cycle of the seasons pass several times unnoticed, that it feels the irresistible urge to return to the ocean of its birthplace.

Yet one cannot stress too much this distinction between external and internal factors, for it has to be noticed that an external periodicity may become enregistered in the organism and may set up within it a corresponding physiological rhythm capable of independent action. This is beautifully illustrated by the observation of Bohn (1910) that the marine worm *Convoluta roscoffensis* retains, for a time, its tidal rhythm in the still water of the aquarium, ascending and descending in the tank as if still under the influence of the ebb and flow. Similarly, Periwinkles are active at high tide and quiescent when the water has receded: in the laboratory they can be reactivated by shaking, even if in a dry environment, but Bohn (1905) has shown that this is much more easily done at the time corresponding to high tide in the sea whence the molluscs were removed. (A similar phenomenon has been recorded in the case of plants with a diurnal rhythm when artificially subjected to different conditions of light and darkness.) In like manner one may well suppose that in those animals which are annually reproductive at a certain season the physiological periodicity includes an element of alternation which would be natural to an animal not living under seasonal conditions, and an element of rhythmic response to the periodicity of the outer world.

Cyclical Phenomena

A different kind of periodicity is shown in the race rather than in the individual, and is from its nature likely to be the result of external conditions rather than of any internal rhythm. This is the periodicity occurring in the fluctuations in the numbers of animals of various kinds in cycles of several years. The subject has recently been reviewed by Elton, who has brought together a large mass of evidence upon it: following him, some brief account

may here be given in so far as the matter is relevant to the present question.

The populations of many species show a tendency to wax and wane in a more or less regular manner through cycles of a few years in length. This is notably the case with certain small rodents : the instance of the Lemming has already been discussed, and similar fluctuations are known to occur among various species of rabbits, mice, and so on. Every few years the increase in numbers leads to over-population : this in its turn is generally followed by an epidemic of some bacterial disease, which speedily reduces the population to the lowest ebb—and the cycle begins again. Incidentally, as in the case of the Lemming in south Norway and elsewhere, the over-population may give rise to immigrations into other districts, these being the movements which give the matter special interest here.

Elton has shown that these fluctuations show a regular although of course not absolutely accurate periodicity. An average cycle of 3·6 years is usual in the case of the small rodents of Arctic and sub-arctic regions, while one of about 11 years is usual in lower latitudes. In some cases both periodicities appear to exist in the same species, one being masked by the other and only discoverable on mathematical analysis of the figures.

What may be the cause of the short cycle of three and a half years it seems difficult to say, but the longer period may with some confidence be ascribed to the effects of the climatic cycles related to the periodicity of sun-spot maxima, which varies from 9 to 13 years but shows a regular average of 11·2. These sun-spot changes indicate variations in the energy output of the sun and thus in the mean temperature of the earth. That there are regular climatic cycles following the same period seems to be established, although their existence may be obscured by the complex and inconstant nature of actual weather phenomena. The separate factors concerned in climate may fail to show any regular periodicity, but, as Elton points out, the total effect of climate may be best judged by manifestations which integrate these factors : such are, for instance, the changes in the level of great lakes, in which the 11 year period has been demonstrated, and fluctuations in plant and animal life. The effect of the 11 year period has been well shown, over a long stretch of time, by curves constructed from the annual growth-rings of the famous Red-wood or Sequoia trees of North America,

average figures from a number of trees being utilised for the purpose.

Slight although the climatic fluctuations may seem, they are nevertheless sufficient to have important effects on plant and animal life : indeed the variation in the mean temperature of the earth is sufficient to make a difference of 80 miles in the position of an isotherm in different years, a change which obviously has biological significance. The effect of climate on the small mammals may be a direct one, or may well be, in part or whole, exercised through the influence upon their food supply. It is interesting to note, too, that the larger mammals which prey on the small rodents are themselves affected by the fluctuations in the numbers of the latter : thus the periodicity shown by the population fluctuations of the Lemmings on the Barren Grounds of Canada are reflected in the annual returns of Red Fox skins obtained by the Hudson Bay Company ! Predatory birds may be similarly affected, and the increase in Short-eared Owls in the south of Scotland at the time of the "plague" of Field-Mice there in 1892–3 is a well-known instance. The effects may be of a still less direct nature, as is shown by the statement that in Greenland the Ptarmigans and other birds benefit by a Lemming year because they are then left alone by the Arctic Foxes : but the next year, when the Lemming population has been decimated and Foxes are plentiful, is a bad one for the birds.

It is probable that there are also much longer cycles, but what the biological results of these may be is for the most part a matter of mere speculation.

This short account of a very important biological subject must here suffice : for the present purposes it is only the migratory movements to which these cyclical population fluctuations sometimes lead that are wholly relevant. Mammals and insects have already been dealt with from this point of view, and certain ornithological examples will be discussed in a subsequent chapter.

Orientation and "Homing"

Animals which perform regular migrations must necessarily possess a well-developed faculty of orientation and power of finding their way. This is well illustrated by the "homing" powers which many animals display. To begin with a lowly example, the Limpet (*Patella vulgata*), according to Ainsworth Davis, frequently leaves its usual scar on

the rock surface and returns to it with great accuracy, orientating itself on the mark in the same position as before : it can find its way back if removed to a distance of as much as three feet.

The question of homing among insects has formed the subject of various experiments with Bees and Wasps, some of the results of which have been conveniently summarised by McDougall. It was shown by Lubbock that Bees depend largely on vision, and that uncertainty is caused if the form, position or colour of the surroundings of the hive is altered. Bethe propounded the view that Bees when laden with honey become positively tropistic to some unknown form of energy radiating from the hive, but Van Buttel Reepen showed that they return to the place after the removal of the hive itself. In various experiments it has been found that homing fails to occur if the insects are removed beyond their normal zone, or into an unexplored arid region happening to lie in one direction, or out from the shore of an adjacent lake : it also does not take place after dark. Yung, for instance, has described an experiment in which twenty Bees were taken six kilometres from their hive and there liberated : seventeen found their way back, but when these seventeen were taken three kilometres out over the adjacent Lake of Geneva next day they failed to return. It is said, however, that even with their eyes obscured Bees have some power of " homing." Similar studies of Wasps have been recorded by Fabre and by the Peckams.

Among Fishes, marked Salmon, for example, have been shown to return to the identical rivers in which they were born. Mammals have also undoubtedly well-developed powers of this kind, and Reindeer follow definite routes in their migrations. In Birds the " homing " faculty probably reaches its highest development, and in a subsequent chapter it will be necessary to return to the subject and to deal with it in more detail.

The term " homing," however, does not cover the whole problem of direction-finding in migration, and it is a sufficient definition only in those cases where there is a single fixed " home " to which there is regular return after an interval of more or less nomadic movement. In the more regular types of migration, as has been noted, there are two fixed localities between which the animals alternate, and these cases accordingly present the problem of how the second home is found on the occasion of the first journey thither. How does the larval Eel unaccompanied by any

adults find its way from the open Atlantic to the rivers and ponds of Europe? How do young birds travelling without their parents find the winter quarters of their species? At the moment, however, it is necessary only to make the point that this and other questions which are about to be discussed in the particular case of Birds have an application to other kinds of animals which also perform movements of a migratory nature.

Hibernation as an Alternative

Migration, as has been said, is in many cases a means of avoiding unfavourable seasonal conditions, but there are many examples of animals which achieve the same end by very different means. Where the conditions are unfavourable at a given season the animal may either migrate to a locality with a different climate or it may remain where it is and modify its manner of life to suit the altered circumstances. The power of remaining in a state of almost suspended animation during the winter or during a period of drought is characteristic of plants, but has also its close counterpart at many levels in the Animal Kingdom. Examples of winter sleep are to be found in such different groups as insects, molluscs, amphibians, reptiles, and mammals, and among fresh-water fishes there are cases in which periods when the pools are dry are survived in a similar way. The hibernation of certain mammals—so familiar an animal as the Hedgehog (*Erinaceus europæus*) is a case in point—is especially interesting, for here one is dealing with warm-blooded animals in which health is ordinarily dependent on the maintenance of a certain body-temperature independently of external conditions: mammals which hibernate, however, are but imperfectly warm-blooded, and during hibernation in a confined space are able to withstand some degree of loss of heat which is not made good by bodily activity.

No instance of hibernation in the case of birds is known to science, and there is no valid reason for suspecting that it ever occurs. Nevertheless, it is not so long ago that so excellent a naturalist as Gilbert White was obsessed, in common with many of his contemporaries, with the idea that hibernation, particularly in the case of the Swallow (*Hirundo rustica*), might play an important part as an alternative to migration. White was particularly influenced by the frequent phenomenon of the few " early Swallows "

which appear some time before the main contingents arrive and are no more seen if wintry weather should recur in the meantime. The idea, of which an early mention is to be found in the writings of Aristotle, dies hard even to-day, and every now and then some imperfect piece of evidence in its favour is recorded—cases, for instance, of birds lingering in autumn being overtaken by hard weather and being found in a comatose condition, really moribund rather than dormant. The further idea that the place of hibernation was in the mud at the bottom of reedy ponds was regarded with sufficient seriousness in the time of John Hunter, the famous anatomist, for him to examine it scientifically: appreciating the value of experiment, he confined Swallows in a conservatory one autumn, providing them with water, reeds and mud, and the result naturally confirmed his scepticism. With better knowledge of bird-migration it is now possible to dismiss these theories as lightly as those once popular notions that birds became transformed into other species in winter or that there is migration between the Earth and the Moon.

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PART I

AN OUTLINE OF BIRD-MIGRATION

THE PRINCIPAL KNOWN FACTS SUMMARISED

" Some creatures can make provision against change without stirring from their ordinary haunts ; others migrate, quitting Pontus and the cold countries after the autumnal equinox to avoid approaching winter, and after the spring equinox migrating from warm lands to cool lands to avoid the coming heat. In some cases they migrate from places near at hand ; in others they may be said to come from the ends of the world, as in the case of the Crane, for these birds migrate from the steppes of Scythia to the marsh lands south of Egypt, where the Nile has its source."

ARISTOTLE, *Historia Animalium*, VIII.
(*Trans.* D'Arcy W. Thompson ; Oxford, 1910.)

CHAPTER I

GENERAL FEATURES OF BIRD-MIGRATION

" Who can recount what transmigrations there
Are annual made ? What nations come and go ?
And how the living clouds on clouds arise ?
Infinite wings ! Till all the plume-dark air,
And rude resounding shore are one wild cry."

JAMES THOMSON, " The Seasons " (Autumn).

The essential principle of migration—Different degrees of migration—Differences within the limits of a species—Differences even in a given area—Only one kind of migration, but different aspects depend upon the relative position of the observer—Terminology of the migratory status of species—Migration to and in the Southern Hemisphere—Northern and Southern Hemispheres compared—Migration found among birds of all kinds—Directions of flight—The nature of the routes followed—Times of migration—Autumn and spring movements compared—General impressions : Vastness, Complexity, and Regularity.

IN its essentials the migration of birds consists of periodical movements between two alternative habitats, a summer area and a winter area. Of these the former habitat is the breeding area and the latter is an area of non-reproductive life. It is an axiom that every bird breeds in the coldest part of its normal range, which is not necessarily the most northerly part—or in the Southern Hemisphere the most southerly part—as climate is by no means wholly a matter of latitude.

The summer area is almost always clearly defined, and there is much evidence that individual birds commonly return to the same breeding localities year after year with a high degree of exactness. In the most highly developed forms of migration the winter area may be almost or quite as definite, although there is much less evidence on this point, while in other cases the autumn movements may not have so constant a goal. There are also movements which are scarcely true migrations, but are rather of the nature of wanderings in which the breeding locality is the only fixed point.

The distance separating the two terminal areas of migration varies greatly in different cases. Some mountain birds

merely descend from the upper slopes to the valleys below for the winter, and in other cases movement is only from inland breeding localities to the more open conditions of the coastal zone of the same country. In speaking of migration, however, one usually has in mind those movements which involve passage from one entire area to another, and in which there is more than a change of altitude or a variation of local conditions. Nevertheless, it is impossible to draw a sharply dividing line, for one finds movements of every intermediate degree. Migration may be merely a matter of a few hundred miles within the limits of a single country, or from one country to another, and possibly over some narrow intervening sea. Or migration may be from high latitudes to the tropics. Yet again, migration may be from the Arctic Zone right across the equatorial belt to the temperate regions of the Southern Hemisphere, and it may be noted that when this happens the migrants do more than find a milder climate—they keep perpetual summer, the incidence of the seasons differing by six months beyond the Equator.

Many kinds of birds are very widely distributed, and it thus happens that the individuals inhabiting different parts of the range of a species at a given season are subject to very different conditions and are migratory in varying degree. In some cases migration may be wholly within the total summer range of the species, the birds from the colder parts withdrawing in winter to the warmer parts where their native kindred are stationary. In other cases the summer range and the winter range may overlap so that there is an intermediate zone where the species is known throughout the year, and at either side of it an area in which the species is found only at one season or the other. In still other cases the whole summer area and whole winter area of a species may lie far apart, with an intervening tract in which the species occurs only as a bird of passage twice a year.

It follows from what has just been said, that a species must often include individuals which are migratory in very different degrees, and even individuals which are migratory and others which are stationary. More than this, birds of the same species and native to the same locality may not all migrate to the same extent, or some may be stationary while others are migratory. Nor is it by any means certain that a given individual bird will behave in exactly the same way in successive years. So it happens that there is every

gradation between species of which all the individuals forsake their entire summer area completely and regularly, and species of which some individuals in some parts of the range sometimes migrate.

There is in principle only one kind of migration, namely that which was defined broadly in the opening paragraph of this chapter, but the observer at a given place sees different aspects of it which depend upon his position relatively to the range of the different species with which he is concerned. He sees the events in cross-section, so to speak. If he be in the exclusively summer area of a species the bird is to him a " summer visitor," if in its exclusively winter area it is to him a " winter visitor." If he be in a place lying between the separated summer and winter areas the species is to him a " bird of passage " : and if he live where the summer and winter ranges overlap he is apt to describe the bird as " resident," and to have difficulty in detecting the migrations which some or even all of the individuals may nevertheless perform.

In an area in which a species is found all the year round the migratory movements are naturally difficult to disentangle. Sometimes there may be seasonal variations in numbers, and sometimes the existence of distinguishable geographical forms or races provides a clue ; but without these aids only a detailed study of the movements themselves will avail. A convenient terminology is also lacking to give the idea clear expression. The labels " summer visitor," " winter visitor," and " bird of passage " are free from ambiguity in those cases where they express the whole truth, provided always that they be used with reference to some given area. The term " resident," however, is rather to be avoided—even if qualified by the expression " as a species "—except for those truly non-migratory birds to which it rightly belongs. The terms " partial migrant " and " individual migrant " are also open to objection on the score of ambiguity, for they should apply to cases where some individuals are migratory and others are not, and do not properly cover cases where all the individuals are migratory and one set completely replaces another with the alternation of the seasons. To express the whole truth with exactness it is necessary, under circumstances of this kind, to describe a species fully as being in a given area, say, " partly resident, partly summer visitant." It may also be noted that to every part of its migratory range except its extreme limits any species is necessarily a bird

of passage in addition to whatever other status it may have.

As already mentioned, some migrants which are summer visitors to northern lands perform the paradox of "wintering" in the summer of the Southern Hemisphere. Not content with merely the mild winter of the northern subtropics they traverse the Equator, and so find a second temperate summer. From the northern point of view they are "winter visitors" to the south, but there they are in fact summer visitors. The interesting point, however, is not this breakdown in the terminology, but the fact which emerges that these birds are in the south summer visitors which do not breed, and which are living there their ordinary non-reproductive life while the birds native to the area are busy with the tasks of their breeding season.

Although northern migrants do not have a second breeding season in the summer of the Southern Hemisphere, it may happen that some birds of a given species lose their true migratory status and become resident in what is for most of their fellows the winter area. There is some evidence that this has taken place in the case of the Bee-eater (*Merops apiaster*). In cases of this kind differentiation into geographical forms may be expected to follow, in course of time, the segregation of breeding areas.

There is, of course, migration in the Southern Hemisphere just as in the Northern, birds native to southerly lands migrating towards the Equator on the approach of winter and returning in spring. Thus, for example, the Welcome Swallow (*Hirundo neoxena*) is the herald of summer in Tasmania in the same way that our own Swallow (*H. rustica*) is in Britain. It follows, therefore, that in these countries the spring sees the arrival of two kinds of summer visitors—the native birds coming for the breeding season, and the birds which have fled the winter of the Northern Hemisphere. Birds native to the Southern Hemisphere, however, do not as a rule migrate to so great an extent as these northern birds, and so it happens that almost no southern birds "winter" in the summer of the higher northern latitudes, and that the complication just described is practically absent from the migratory phenomena which are witnessed in Europe. The only exceptions appear to be some of the southern Petrels which come far across the Equator during their oceanic wanderings in the non-breeding season: the Great Shearwater (*Puffinus*

gravis), for example, is native to the South Atlantic, and visits British seas during what is here the late summer. The absence of the highest degree of migratory performance among southern birds is itself a point of some interest.

It has to be remembered not only that the total area of land in the Southern Hemisphere is much less than that in the Northern Hemisphere, but also that there is practically nothing in the south corresponding to the vast tracts of sub-arctic territory in Europe, Asia and North America, which provide the summer homes of so many notably migratory species. Apart from the Antarctic Continent, which is isolated by a wide belt of ocean and is visited by a relatively small number of species representing only five of the natural orders, only South America of the southern continents extends beyond the fiftieth parallel. Thus Africa extends no further south of the Equator than it does north, Tasmania and the South Island of New Zealand lie in latitudes corresponding respectively to those of Spain and of southern France, and Patagonia lies no nearer the pole than does Scotland. These facts are themselves perhaps sufficient explanation of the lesser degree to which migration is developed among native southern birds.

It should be mentioned, however, that some parts of the northern Tropics are visited by birds which breed near, or south of, the Equator ; while in the same area and at the same time other species may be breeding which go south in their off-season. The matter is complicated by the fact that in these regions breeding in general is not restricted to any one time of year : there is, of course, no summer and winter in the ordinary sense. It seems probable that migration occurs among native tropical birds chiefly in regions where there are neighbouring areas of very diverse character in which the incidence of wet and dry seasons has different effects. Although information on the subject is scanty, one is inclined to think that in those parts of the Tropics where the conditions are more uniform the native birds are almost wholly stationary. In any event, it is not known that any native tropical birds perform movements of such an extent as to take them beyond the limits of the Tropical Zone in their off-season.

Reference may also be made to two minor complications in the general migration picture. One is that immature or other non-breeding individuals may remain in the winter quarters, or in some intermediate region, during the breeding

season of the species. Another is found in the fact that in summer some birds visit regions which lie beyond the breeding area in the direction opposite to that of the winter quarters. It is, for instance, typical of various species of Heron in North America that the young disperse in the late summer, many of these reaching places some hundreds of miles north of the breeding limit, before the true migration, in a southward direction, sets in. Furthermore, in the case of one migratory species, the Snowy Egret (*Egretta candidissima*), non-breeding adults are for some reason frequently found throughout the summer 500 or 1000 miles northwards of the nesting area. This constitutes a slight exception to the general rule that every bird breeds in the coldest part of its range. It may be added in this regard that some more or less non-migratory birds, such as certain Gulls, may disperse in winter over an area which extends some distance both to the north and to the south of the restricted breeding locality.

Migration is not restricted to any particular systematic group of the class Aves. Except among the running birds of the Ostrich tribe, the Ratitæ, there is scarcely an order which does not include notable migrants : even the flightless Penguins are by no means to be excluded from this statement. To realise the fact one has only to think of such diverse examples as the Swallow and the White Stork, the Cuckoo and the Golden Plover, the Arctic Tern and the Quail, the Rough-legged Buzzard and the Turtle-Dove. The Parrots constitute perhaps the most important group which is largely restricted in range to the tropics and sub-tropics, but even among them there are migratory species, one of which, in days when it was more numerous, used to visit Canada in summer. The Humming-birds, too, though chiefly found in tropical and sub-tropical America, include two species which in summer reach sub-arctic latitudes in Canada and Alaska.

Yet, although migration is widespread among birds, there are very many species and many whole families, chiefly those confined to the Tropics, which are believed to be wholly stationary. In high latitudes there are certainly few species which do not migrate. The Spitzbergen Ptarmigan (*Lagopus mutus hyperboreus*) has been described as the hardiest of all birds, and for some two-thirds of the year it lives in darkness and in burrows under the snow. Even this, however, seems to be surpassed by the Emperor Penguin (*Aptenodytes forsteri*), which not only lives but

breeds on the ice during the perpetual night and tremendous frost of the Antarctic winter.

Birds which are summer visitors in Europe commonly winter in the Mediterranean region or in equatorial Africa, the greater travellers reaching South Africa. Those which are summer visitors in Asia variously reach Africa, the Indian region, and Australasia. For North American birds the usual winter quarters are naturally in Central and northern South America, and in southern South America in extreme cases. Some northern species, such as the Knot (*Calidris canutus*), which are circumpolar in their summer range, have an immense non-breeding distribution in the Southern Hemisphere—to the Cape, India, Australia, New Zealand, and Patagonia.

As has already been stated, birds native to the Southern Hemisphere do not, with unimportant exceptions, penetrate to the temperate regions north of the Equator, to " winter " in the northern summer. Species which are summer visitors in the southern parts of Africa, South America, and Australasia thus go no farther than the equatorial regions of their respective continents. Summer visitors to New Zealand winter in Australia, New Guinea, and the Polynesian Islands. To find winter quarters the birds native to the Antarctic Continent must cross the circumpolar ocean, unless, like the Penguins, they are capable of a pelagic life, and need go no farther than the northward winter limits of the pack-ice.

The direction of migration flight is not necessarily from north to south and *vice versa*, for, as has already been noted, a different climate may often be found with little or no change in latitude : there is, indeed, in Europe a great deal of migration on an almost due east and west line. Nor does flight necessarily follow the shortest line between the two terminal points. On the subject of the nature of the routes which are followed information is, however, somewhat scanty, and it is probable that on the whole too much has been made of the idea that migration is restricted to certain narrow and well-defined flight-lines : nevertheless, the general directions of flight remain constant year after year. Coast-lines are certainly followed to a great extent, and much migration may follow the valleys of important rivers : on the other hand, the advance across stretches of sea and land is often made on a broad front. High mountain ranges are often surmounted, and wide expanses of sea are regularly crossed in some parts of the world.

The directions followed in the same region by birds of different species, or even by individuals of a single species, are sometimes widely divergent. Thus in Europe the general trend of autumn migration for most species is south-westwards: the White Stork, however, largely follows a south-easterly line from Northern Europe to the Levant. In autumn many birds reach the south-eastern counties of England on an east to west line of flight, and in doing so they cross the path of others of their kind flying southwards towards the Continent along the eastern seaboard of Great Britain. More remarkable still, St. George's Channel is crossed in spring from south-east to north-west by summer visitors to Ireland, arriving from Southern Europe by way of the south of England, and also from north-west to south-east by departing winter visitors bound, by way of southern England, for breeding places farther east: even birds of the same species may participate in these opposite and practically simultaneous movements over what is at this point the same course.

One is apt to speak of migration as an event which occurs twice in the year, once in spring and once in autumn, but this is only a partial truth. The migration of any given species may extend over a period of months, the arrival in spring in the warmer parts of the summer area taking place much in advance of the date of arrival at the farther extremity of the breeding range. Then again, some species are in general much earlier migrants than others, so that the migration season as a whole is still further prolonged. On the autumn journey, too, young birds of the year frequently travel in advance of their parents: in the case of the Cuckoo (*Cuculus canorus*), which neither broods its own eggs nor rears its own young, the order is reversed and the autumn migration of the adults is much earlier than that of the young. In truth it may be said that there is almost no time in the cycle of the seasons when movement of some kind is not taking place. The latest arrivals in the colder countries complete their journey only a little before midsummer, and by that time the first young birds of earlier species farther south are almost ready to depart. Similarly, the winter movements are often so protracted that they almost overlap the first spring movements in the reverse direction.

The autumn movements are on a grander scale than the spring ones, for the number of the migrants, increased by the young of the year, is then at its maximum. The period

of migration is more protracted also, for the autumn migration begins with very early departures just after midsummer, and is extended through the winter to a varying extent by "weather movements" which follow specially severe conditions late in the season. On the autumn journey, too, travelling is often undertaken in a more leisurely fashion, and has not the urgency of the spring return to the breeding areas.

Of the general impressions which one may obtain of the phenomenon of bird-migration perhaps the first is one of vastness. Thousands of species and untold millions of individuals take part in migration. The movements cover almost all parts of the globe, and the individual journeys performed twice a year amount in some cases to thousands of miles on each occasion. There is scarcely a time in the year at which movement of some kind is not in progress.

And in addition to vastness there is complexity. Different species migrate at different times and in different degree. Within the limit of a single species there may also be great differences between individuals. In a single country a given species may be represented by individuals which are respectively summer visitors and winter visitors thereto, and by others which are birds of passage and by still others which are stationary. Then there is the fact that some northern birds migrate so far that they spend a second summer in the temperate regions of the Southern Hemisphere while the native birds are breeding there, and the additional fact that there is scarcely any counterpart to this among migratory birds which breed south of the Equator. Again there are the varying directions of migration flight, so complicated that simultaneous streams may cross each other at right angles or even proceed in exactly opposite directions over the same course.

But despite the vastness and the complexity of the phenomena there is also a wonderful degree of regularity and accuracy. Individual birds return accurately to the same summer locality in a subsequent year although journeying half across the world and back in the interval. In a given area species depart and reappear annually at almost exactly the same dates. The same general directions of flight are followed on each occasion. In short, the phenomena of migration are repeated annually on the selfsame lines: the component events recur regularly according to plan. There is nothing fortuitous about them, and there is

relatively little difference between one year's movements and another's, even although the climatic conditions may vary widely.

There is, then, a vast complex series of events recurring annually with a truly amazing degree of regularity.

CHAPTER II

BRITISH ASPECTS OF BIRD-MIGRATION

" Unknown, enormous leagues of air,
England's sweet summer narrowing on,
Her lovely pastures—nought their care
But this strange ardour to be gone."

WALTER DE LA MARE, " Martins : September."

British movements as an example of migration in a particular area—Characteristics of the British Isles as a migration area—*British status of various migratory species :* Summer visitant species—Winter visitant species—Species which are solely birds of passage—Migratory species which are represented by some individuals throughout the year—Stationary species—Local differences—Distinguishable geographical races. *Geographical aspects :* Analysis of the main British movements—Directions of Movements. *Seasonal aspects :* The sequence of events throughout the year.

IN the preceding chapter the phenomena of bird-migration were surveyed in broad outline from a world-wide point of view. For the purposes of a more detailed examination it is necessary to select a concrete case, and in this chapter the British Isles are accordingly taken as an example of a geographical area in which particular migration movements may be observed.

The general characters of the British Isles as a migration area depend partly on their climate and partly on their position in relation to the European land-mass as a whole. In very high latitudes migration is a relatively simple phenomenon, all the birds being purely summer visitors : near the Equator the general tendency is for the native birds to be stationary, and migration in some parts of the Tropics thus seems to be largely confined to species which breed in other regions. In a temperate country, however, the position is a complicated one intermediate between these two extremes : a great many birds are migratory, probably the great majority, but in different degrees and with movements which have all manner of geographical relations to the country. Thus the British Isles are for some species a summer area, for some a winter area, and for others a mere point on the route between the two. For a

great many species, also, the British Isles lie in the zone where the summer and winter areas overlap, and these species are accordingly represented throughout the year by individuals of varying migratory status.

There is also the fact that the British Isles enjoy a much more temperate climate than many parts of the Continent which lie within the same degrees of latitude. As a result of this it happens that they serve as a winter area not only for birds from farther north but also for birds which are native to regions lying to the east and even south-east. This is a point to which further attention will be given in considering the directions of migration flight in the area.

A beginning may be made by considering what kinds of migratory species have principally to be dealt with in the British Isles, and into what categories they naturally fall according to their status as migrants from a British point of view.

The British Status of Various Migratory Species

The following species are typical summer visitors to the British Isles and are normally completely absent therefrom in winter. Those of them which also visit countries farther north occur, in addition, as birds of passage on their way to and from these parts of their summer range: among the few exceptions the Nightingale and the Kentish Plover may be named as species which reach the limit of their range in the British Isles.

Ring-Ouzel (*Turdus torquatus*); Nightingale (*Luscinia megarhyncha*); Wheatear (*Œnanthe œnanthe*); Whinchat (*Saxicola rubetra*); Redstart (*Phœnicurus phœnicurus*);

Whitethroat (*Sylvia communis*); Lesser Whitethroat (*S. curruca*); Blackcap (*S. atricapilla*); Garden-Warbler (*S. borin*); Wood-Warbler (*Phylloscopus sibilatrix*); Willow-Warbler (*P. trochilus*); Chiffchaff (*P. collybita*); Sedge-Warbler (*Acrocephalus schœnobœnus*); Reed-Warbler (*A. scirpaceus*); Marsh-Warbler (*A. palustris*); Grasshopper-Warbler (*Locustella nævia*);

Spotted Flycatcher (*Muscicapa striata*); Pied Flycatcher (*M. hypoleucus*);

Yellow Wagtail (*Motacilla flava*); Tree-Pipit (*Anthus trivialis*);

Red-backed Shrike (*Lanius collurio*);

Swallow (*Hirundo rustica*); House-Martin (*Delichon urbica*); Sand-Martin (*Riparia riparia*);

Wryneck (*Jynx torquilla*);

Swift (*Apus apus*);

Nightjar (*Caprimulgus europæus*);

Cuckoo (*Cuculus canorus*);
Montagu's Harrier (*Circus pygargus*); Hobby (*Falco subbuteo*);
Garganey (*Anas querquedula*);
Turtle-Dove (*Streptopelia turtur*);
Quail (*Coturnix coturnix*);
Land-Rail (*Crex crex*);
Stone-Curlew (*Burhinus œdicnemus*); Dotterel (*Charadrius morinellus*); Kentish Plover (*C. alexandrinus*); Common Sandpiper (*Tringa hypoleucos*); Whimbrel (*Numenius phæopus*); Red-necked Phalarope (*Phalaropus lobatus*);
Sandwich Tern (*Sterna sandvicensis*); Common Tern (*S. hirundo*); Arctic Tern (*S. macrura*); Roseate Tern (*S. dougallii*); Little Tern (*S. albifrons*);
Arctic Skua (*Stercorarius parasiticus*).

This list is not exhaustive but it is thoroughly representative. It includes most of the examples which can be called common and also a few relatively uncommon birds which have been named because they belong to groups which would not otherwise be represented. It will be seen that Passerine birds predominate, and that of these the Warblers are the most numerous group and the Thrushes and the Swallows perhaps the next most important. Most of these are either wholly or largely insectivorous birds, and the same applies to the miscellaneous group comprising the Wryneck, Swift, Cuckoo, and Nightjar. The groups coming next in point of numbers are the Terns and the Waders, but of the latter there is only one really common representative, the Common Sandpiper. There are in addition two Birds-of-Prey, neither of them very common; a rather uncommon representative of the Ducks, the Garganey; one Pigeon; one Gallinaceous bird; one Crake; and one Skua.

Evidence is only now beginning to be obtained as to the exact winter quarters of individual birds which visit the British Isles, and in most cases all that is known is the winter range of the species as a whole. The winter range of the Common Sandpiper, for instance, extends from Southern Europe to South Africa, and to which part of this vast area the individuals native to the British Isles may go is as yet unknown. The winter range of the Arctic Tern extends from the tropical Atlantic to the Antarctic, where it was seen in the Weddell Sea up to 74° 1′ S. lat. by the Scottish National Antarctic Expedition under Bruce: as it is known to reach 82° N. lat. in summer, its latitudinal

range is the greatest known for any vertebrate animal and amounts to some 11,000 miles. Many of the other species named above have a winter range which includes a great part of Africa: the Swallow, for instance, is found from the northern Tropics to Cape Colony. Others have a more restricted area: the Ring-Ouzel is found in winter in Southern Europe and northern Africa, and the Turtle-Dove in Equatorial Africa. It must also be remembered that many of these species have a summer range extending eastwards into northern Asia and are found in winter in southern Asia as well as in Africa.

The following species are typical winter visitors to the British Isles; they are normally absent therefrom in summer, although non-breeding birds may occasionally remain, and in a few instances there are isolated records of breeding. Those of them which visit countries still farther south may also occur as birds of passage on their way to and from these parts of their winter range, and this is indeed for some of them the predominant status.

Redwing (*Turdus musicus*); Fieldfare (*T. pilaris*); Black Redstart (*Phœnicurus ochrurus*);

Brambling (*Fringilla montifringilla*); Mealy Redpoll (*Carduelis linaria*);

Shore-Lark (*Eremophila alpestris*);

Great Grey Shrike (*Lanius excubitor*);

Waxwing (*Bombycilla garrulus*);

Rough-legged Buzzard (*Buteo lagopus*);

White-fronted Goose (*Anser albifrons*); Bean Goose (*A. fabalis*); Pink-footed Goose (*A. brachyrhynchus*); Barnacle Goose (*Branta leucopsis*); Brent Goose (*B. bernicla*); Whooper (*Cygnus cygnus*); Bewick's Swan (*C. bewickii*); Goldeneye (*Bucephala clangula*); Long-tailed Duck (*Clangula hyemalis*); Velvet Scoter (*Oidemia fusca*); Smew (*Mergus albellus*);

Grey Plover (*Squatarola squatarola*); Turnstone (*Arenaria interpres*); Jack Snipe (*Lymnocryptes minimus*); Purple Sandpiper (*Calidris maritima*); Knot (*C. canutus*); Sanderling (*Crocethia alba*); Bar-tailed Godwit (*Limosa lapponica*);

Glaucous Gull (*Larus hyperboreus*); Iceland Gull (*L. glaucoides*);

Great Northern Diver (*Colymbus immer*); Red-necked Grebe (*Podiceps griseigena*);

Little Auk (*Alle alle*).

This list, also, is not exhaustive but is thoroughly representative. Passerine birds are represented by three Thrushes,

two Finches, and three other species which are relatively uncommon. The Geese and Ducks are the most important group, and after them the Waders. There are also two members of the Grebe and Diver group, one Auk, and one Bird-of-Prey.

In summer most of these birds are to be found in northern Continental Europe and western Siberia, as in the case of the Fieldfare, for example. Others have an even more northerly breeding area, the Barnacle Goose in Greenland and Spitzbergen, and the Knot in northern Siberia, Greenland and Arctic America. Others, like the Purple Sandpiper, are in summer found also in Iceland and the Faroes, while the Red-necked Grebe breeds just across the North Sea in southern Scandinavia. The Black Redstart comes from Central Europe and is not found regularly in summer anywhere to the north of the British Isles : it is more numerous here as a bird of passage than as a true winter visitor.

The following species are typical of those that are wholly birds of passage to the British Isles, which lie between their summer and their winter areas. Thus they normally occur only during the spring and autumn migrations, although a few may sometimes linger during the winter or summer : (the Ruff and the Wood-Sandpiper have been recorded as breeding on a few occasions ; the Ruff, the Black-tailed Godwit, and the Black Tern formerly bred regularly in the British Isles).

Bluethroat (*Luscinia svecica*) ; Yellow-browed Warbler (*Phylloscopus humei*) ;

Lapland Bunting (*Calcarius lapponicus*) ; Ortolan Bunting (*Emberiza hortulana*) ;

Great Snipe (*Capella media*) ; Ruff (*Philomachus pugnax*) ; Little Stint (*Calidris minuta*) ; Curlew-Sandpiper (*C. ferruginea*) ; Wood-Sandpiper (*Tringa ~~ochropus~~*) ; Spotted Redshank (*T. erythropus*) ; Black-tailed Godwit (*Limosa limosa*) ; Grey Phalarope (*Phalaropus fulicarius*) ;

Black Tern (*Chlidonias niger*) ;

Pomatorhine Skua (*Stercorarius pomarinus*) ; Long-tailed Skua (*S. longicaudus*).

To make up even this short list it has been necessary to include birds which are much less common in this country than most of those named as examples of the two previous categories. There is indeed scarcely one of them which could be described as common even during the restricted periods when its presence is to be expected. The group best represented is that of the Waders, in which the necessary quali-

fications of a restricted northern summer range and a distant winter area are most typically present. The list could of course be increased in length, and as to the number of groups represented, if one were to include those species which occur in very small numbers or at irregular intervals as wanderers from some stream of migration of which the main course lies elsewhere. It could also be increased by the addition of species which are largely but not wholly birds of passage ; examples are the Black Redstart, already mentioned as a winter visitor in small numbers, and the White Wagtail (*Motacilla alba alba*), of which a few remain irregularly to breed in the British Isles.

To take the two best examples, the Little Stint breeds on the north coast of Europe and Asia and on the Arctic lands beyond, and is found in winter from Southern Europe to South Africa ; the Curlew-Sandpiper breeds in northern Siberia, and in winter it ranges not only to South Africa but also to India, Tasmania, and Patagonia.

Of the casual visitors which reach the British Isles, usually as irregular birds of passage, several belong to Asia and one or two to Africa, while various kinds of Petrels come from oceanic islands in different parts of the world. Most of these are rarities which are only exceptionally recorded. The list of wanderers from North America, particularly of Sandpipers of various species, is more formidable, and in some cases occurrences are noted with relative frequency. A small amount of migration from high latitudes in North America, probably by way of Greenland and Iceland, to the western coasts of Europe cannot therefore be regarded as altogether abnormal.

The three foregoing categories include only those birds which are as a rule entirely absent from the British Isles during some part of the year. Most of the species which are represented throughout the year to a greater or less extent, however, are also migratory in some degree, but of them it must suffice to name a few typical examples.

There are in the first place certain species which show very great variations in the numbers present at different seasons, and which have therefore what may be described as a predominant status. The Snow-Bunting (*Plectrophenax nivalis*) and such Ducks as the Wigeon (*Anas penelope*) and the Common Scoter (*Oidemia nigra*) may be taken as examples of birds which breed in the British Isles in small numbers, and rather locally, but which are abundant in winter.

More difficult, however, are the many species which are common and widely distributed throughout the year but are nevertheless migratory to a notable extent. The Lapwing (*Vanellus vanellus*) is a good example : some appear to be stationary, some are certainly summer visitors which breed in the British Isles and go farther south in winter, while others are winter visitors and still others are probably birds of passage. The case of the Mallard (*Anas platyrhyncha*) is less complicated : here the native British birds appear to be stationary, but there is a great influx of birds from Northern and Central Europe for the winter. These and other examples will be considered in more detail in the second part of this book, and here it need only be added that they are characteristic of a great deal of the migration in the British area and of the special position of the British Isles as a " half-way house " in the migration area of Western Europe. Other well-known species coming within this category are the Song-Thrush (*Turdus philomelos*), the Starling (*Sturnus vulgaris*), the Hooded Crow (*Corvus cornix*), the Rook (*C. frugilegus*), and the Skylark (*Alauda arvensis*).

Many of the species which are partially winter visitors to the British Isles and partially native thereto, have, not unnaturally, a more southerly breeding range on the Continent than is usual in the case of northern birds which are unknown here in the summer. It is species falling within this category, accordingly, which produce a great part of the movements from Central Europe on an east to west line. It also follows that species which are only partially summer visitors to the British Isles (i.e. also present to some extent at other seasons) have a less southerly range than those which are entirely absent from here in winter : summer visitant individuals of species in this group as a rule migrate no farther than to France, Spain, and Portugal, or at most to north-western Africa.

Only one more category remains to be briefly mentioned. Very few indeed are the British species which can be correctly described as wholly stationary or even as subject only to local movements within the limits of the country. The best examples are undoubtedly the Gallinaceous birds, and of these the Red Grouse (*Lagopus scoticus*) is in this respect the type *par excellence*, in that it has the unique distinction of being altogether unknown abroad. Other well-known examples of species which appear to be practically resident in the strict sense are the Tree-Creeper (*Certhia*

familiaris), the Nuthatch (*Sitta europæa*), the Coal-Titmouse (*Parus ater*), the Green Woodpecker (*Picus viridis*), and the Rock-Dove (*Columba livia*).

It should be noted that throughout the foregoing discussion of the status of various species in the British Isles, the country has been considered as a whole. There are, however, many local differences, and in considering any particular division of the country the terminology would in many cases have to be varied. To England the Snow-Bunting, for instance, is wholly a winter visitor, although in parts of Scotland it is found in small numbers as a breeding species. Of the summer visitors some, such as the Nightingale, reach the limit of their range in the British Isles and are not found in the more northern parts. The question of migration from one part of the country to another, without passage beyond its limits, has also been neglected.

Similarly, it has seemed convenient to speak of species as a whole and to neglect for this purpose the question of the subdivision into distinguishable geographical races which has in recent years been made in the case of so many birds. Among the Passerine species, especially, there is frequently a distinguishable continental or northern form which occurs here as a winter visitor or bird of passage, the British form being in the majority of these cases more or less stationary.

Geographical Aspects

Turning from the question of separate species to that of the British movements as a whole, the different phases may be classified, although not chronologically, in the following manner :—

Autumn

(1) Local movements of native birds within the British Isles, in some cases preparatory to emigration.
(2) Emigration of native summer visitors.
(3) Through migration of birds of passage.
(4) Immigration of winter visitors.
(5) Weather movements, depending upon the severity of the winter.

Spring

(6) Emigration of winter visitors.
(7) Through migration of birds of passage.
(8) Immigration of native summer visitors.
(9) Local movements of native birds returning to breeding haunts.

These phases of the movements overlap in point of time and are not readily separable one from another. In particular, the through migration of birds of passage accompanies respectively the immigration and the emigration of birds which make the British Isles their home for part of the year. Local movements are not in themselves of a special nature, and they are to be distinguished only because they happen to begin and end within the geographical unit with which one is dealing. The weather movements which occur in severe winters take the form of a continuation of many of the ordinary autumn movements: they vary according to the nature and duration of the conditions and to the area affected, being sometimes merely local and at other times involving renewed immigration, passage, and emigration.

In considering the directions of the different movements it will be convenient to deal with the autumn phases: the spring movements naturally follow the reverse directions in the main, but they are in some cases less well known and are possibly not always exact counterparts. The following are the principal directions of migration to and from the British Isles in autumn:

(1) From the north and north-west: Immigration and passage from Greenland, Iceland, and the Faroe Islands.
(2) From the north-east: Immigration and passage from northern Continental Europe (Scandinavia, northern Russia, etc.), Spitzbergen, and northern Siberia.
(3) From the east: Immigration and passage from Central Europe, and from Northern Europe by the same route.
(4) To the south: Passage and emigration to Southern Europe and to Africa.

The immigration from the north and north-west takes place on the north-western seaboard of the British Isles as far east as the Shetlands, and the subsequent passage movements largely follow the coasts—especially the west coast of Great Britain and both sides of Ireland—southwards. The immigration from the north-east strikes the eastern seaboard of Great Britain from the Shetlands to the Humber, and passage continues mainly southwards along the east coast and westwards along the south coast. The immigration from the east strikes the eastern counties

of England which lie immediately north and south of the Thames estuary. Emigration towards the south takes place from the south coast of England.

It may be mentioned that Riviere (1925) has suggested that there may also be some migration on an east to west line in spring, possibly of summer visitors from the south following a more easterly route than usual and then turning westwards from Holland to the south-east of England. The movement has not been observed, but on the Norfolk coast small birds are found resting near the shore in spring in exactly the same way as those which arrive from the east in autumn. An alternative hypothesis is that the birds have come up the coast from the south. The same observer has noted that Swallows may be seen following the Norfolk coast northwards and then westwards both in autumn and in spring : similar phenomena are known elsewhere, but it does not, of course, follow that the two movements are more than locally coincident in their directions.

Apart from minor movements from high levels to low ground, and from inland districts to the coast, the local movements within the British Isles in autumn are southerly and westerly in direction, and include much migration from Great Britain to Ireland. The passage movements through the area, as has been shown, largely follow the coasts, southwards and westwards, from the points of arrival to the points of departure.

With regard to migration in Ireland, Barrington has made an interesting analysis of the spring movements as observed at the light-stations round the coasts. He found that the immigrants are divisible into four main groups, as follows : (1) Those arriving on the south-west, south, south-east, east, and north-east coasts ; (2) those arriving on the south-easterly section only, including some which are noted as arriving only at the extreme south-eastern corner ; (3) those arriving on the eastern section ; and (4) those arriving on the southern section. He suggested that birds in the second group come from the south-west of Great Britain, those in the third from the whole eastern portion of England and Wales, those in the fourth direct from France, and those in the first from all sources.

Seasonal Aspects

For a short period at the end of June and the beginning of July migration is practically in abeyance in the British area, all birds being in their respective native localities here

PRINCIPAL DIRECTIONS OF MIGRATION TO AND FROM THE BRITISH ISLES IN AUTUMN.

Mainly after Eagle Clarke, adapted.

Showing the chief general directions of migration movements in the British area in autumn. The principal directions in spring are similar, but, of course, reversed.

The arrows are intended to show only the general directions of the chief movements. It is not to be understood that the movements are necessarily confined to narrow paths or that there is any lack of branch, tributary, and other subsidiary routes.

or abroad and, if mature and mated, engaged in the tasks of the breeding season. This accordingly forms a natural starting-point for a survey of the sequence of events throughout the year.

Early in July the first signs of the autumn migration are to be noted. The birds moving so early in the season are for the most part youngsters only a few weeks out of the egg, with a smaller number of old birds which have probably not bred or have been unfortunate in doing so. The earliest movements are local ones within the British Isles, representing a preliminary dispersal from the breeding localities. Later in the month the exodus of summer visitors sets in: adult Cuckoos are among the first to leave for the south, and early migrants such as the Swift also leave in some numbers, but for the rest the movement is confined to a small proportion of individuals belonging to species of which the main departure takes place later in the season. Still later in July begin the passage movements through the area of birds, notably Waders, which are summer visitors to regions farther north.

August sees a continuation of the movements begun in July, but as yet no migration on a great scale. The passage of birds which are summer visitors farther north continues, and some of these are now birds which will winter no farther south than our islands. The exodus of our own summer visitors makes further progress, and that of such species as the Cuckoo and the Swift is almost completed before the end of the month.

September is the chief month for the departure of our summer visitors, and by its end many species have completely disappeared for the winter. Passage movements and the immigration of winter visitors have increased in volume, and from about the middle of the month these include migration from the east as well as from the north.

In October the autumn migration is at its height, for this is the chief month for passage movements and for the arrival of winter visitors. Our own summer visitors have nearly all gone already, but birds of the same species which bred farther north, where the breeding season is necessarily later, continue to pass through.

Up to the third week of November the later features of the October movements continue in diminishing volume, and the true autumn migration is then practically at an end.

From November to March, however—and especially in December and January—there occur weather movements

which vary in time and nature according to the meteorological characteristics of the particular year. During this period spells of severe weather give rise to these further movements continuing those of autumn. They are chiefly local, migration to the south and west within the British Isles, including migration from Great Britain to Ireland; but there may also be emigration to the south or immigration from the north and east. It is during severe winter weather that northern species which are rare visitors to the British Isles tend to appear in our area. These weather movements may overlap the spring migration in the opposite direction. Indeed, it not infrequently happens that snow falls heavily on the high ground after birds native thereto have returned for the breeding season, and that these birds are temporarily driven back: these reverse movements are probably purely local in character, however.

Towards the middle of February the spring migration begins. The first movements are local ones within the British Isles, the return of local migrants to their breeding grounds, and migration from Ireland to Great Britain. If the weather conditions are favourable, the second half of the month sees the first immigration of summer visitors from the south, but these are mainly of species which are also known in the British Isles in winter. Emigration to the north and, especially, to the east may also begin late in this month.

In March the local movements are at their height, and so also are the through passage movements of birds belonging to migratory species which are represented here all the year round. The first arrivals of birds of wholly summer visitant species are noted, among these early immigrants being the Wheatear, the Ring-Ouzel, the Chiffchaff, and the Sand-Martin. Emigration of winter visitors on a large scale also takes place.

Nearly all the remaining summer visitant species begin to arrive in April, and the passage of these species to countries farther north also sets in. The emigration of our winter visitant species is continued.

May is the month of the maximum migration in spring. The advance parties of most summer visitant species have already appeared, but now the main bodies arrive. The passage of summer visitors to countries farther north is also at its height. Especially in the first half of the month, there is still much emigration of our winter visitors seeking their summer quarters.

Before June most of our summer visitors are here except that late arrival, the Marsh-Warbler, but there is still much passage through the area, especially of species such as the Mealy Redpoll, Snow-Bunting, and various Ducks and Waders which are bound for the far north. By the end of the month, as has already been noted at the beginning of this review of the migration year, the wheel has turned full circle and all birds are again established in their native localities.

There are of course important differences in dates between one district of the British Isles and another, but here the country has been treated as a whole and the movements have been mentioned under the dates when they are first noted in any part.

In conclusion, although it has not seemed necessary to refer to any authorities for the separate statements in this chapter, some mention may be made of the principal work upon which knowledge of the subject is based, and of some convenient sources of more detailed information on special points. The most important contributions are those made by Eagle Clarke, both for the Bird Migration Committee of the British Association and independently: these have been published in collected and amplified form in a book (1912) which must for long remain the standard work. Further important data have been collected by a committee of the British Ornithologists' Club, under the chairmanship of Penrose, and published in nine reports. Many useful records are also contained in the annual reports on Scottish ornithology compiled by Baxter and Rintoul, and formerly by Paterson, and in the reports on the ornithology of Norfolk made for twenty-nine years by Gurney and now being continued by Riviere. Much information relating to restricted parts of the area may be found in the more modern works dealing with local avifauna, among which those of Nelson, Ticehurst, Gladstone, and Forrest may be named as examples: in regard to Ireland, the works of Barrington and of Ussher and Warren may be mentioned. For summaries of the migratory status of separate species reference may be made to such general text-books as those of Kirkman and Witherby respectively. The data of a new kind which are now becoming available through the exploitation of the bird-marking method are scarcely drawn upon in this chapter, or in the works just mentioned, and will receive special attention in the second part of this book.

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SOURCE OF DATA SHOWN ON MAP.—The map of the directions of migration movements to and from the British Isles is adapted from part of a map of the principal directions of migration in Europe published by Eagle Clarke (1912).

CHAPTER III

MIGRATION IN PROGRESS

" White spirits from the Northland,
Grey clan of Storm and Frost,
Wind-swooping to the Southland
From icy seas blast-tost."

FIONA MACLEOD, "At the coming of the Wild Swans."

Difficulties of observation—Nocturnal migration observed at lighthouses—Heligoland—The Eddystone—Nocturnal migration at sea—Diurnal migration as visible from islands—Starling migration over Heligoland—Swallow migration over Heligoland—Swallow migration in East Africa—Diurnal migration on the Baltic coast—Hooded Crows—Diurnal migration at sea—The Kentish Knock Lightship—Storks in the Mediterranean—Migration in the Southern Hemisphere—Military Starlings in the Argentine—The flightless migrations of the Penguins.

THE general facts of bird-migration in its world-wide aspect have been considered, and the events which occur in the British Isles, selected as a typical area, have been discussed in more detail. Some account must now be given of migration as it may be seen in actual progress by an observer at a particular spot.

In inland districts especially, very little is seen of migration : its existence is often merely to be inferred from the periodical appearances and disappearances of certain species and from the seasonal fluctuations in the numbers of others. The nearest approach to actual movement which is frequently observed is the flocking which takes place in some cases immediately before the autumn departure ; but the flight is usually unobserved—one day the birds are there in noisy excited bands, and the next day many or all have gone. On islands which lie in the path of great movements there may be readily observable changes in the bird population from day to day during the seasons of passage, and some idea of what is taking place may be gathered from observation of the different birds which are congregated for a few hours of rest within the circumscribed area of land available to them. Even in such favoured places as these it may happen that only a little of the migration flight itself is to be seen.

A very great deal of migration takes place by night, and this even in the case of many species which are by no means nocturnal in their ordinary habits. Under most circumstances these nocturnal flights are apparent only from the cries which come down through the still night air, as may happen even in great cities, but only a very little of the vast movement comes to notice in this way. Migration by night is regularly observed, however, at lighthouses and lightships, and the conditions most favourable for this are moonless nights, overclouded sky and slightly misty weather: the rays of the lantern then have a dazzling effect which attracts many migrants within the circle of vision, like moths wheeling round a candle flame, while not a few dash themselves to destruction against the glass.

The naturalist who is fortunate enough to be present at a light-station on a favourable occasion may see such a scene as Gätke describes in the following passage, relating to the lighthouse on the island of Heligoland: "The whole sky is now filled with a babel of hundreds of thousands of voices, and as we approach the lighthouse there presents itself to the eye a scene which more than confirms the experience of the ear. Under the intense glare of the light swarms of Larks, Starlings, and Thrushes career around in ever-varying density, like showers of brilliant sparks or huge snow-flakes driven onward by a gale, and continuously replaced as they disappear by freshly arrived multitudes. Mingled with these birds are large numbers of Golden Plovers, Lapwings, Curlews, and Sandpipers. Now and again, too, a Woodcock is seen; or an Owl, with slow-beating wings, emerges from the darkness into the circle of light, but again speedily vanishes, accompanied by the plaintive cry of an unhappy Thrush that has become its prey."

Even more vivid is the description given by Eagle Clarke of a similar scene witnessed in the autumn of 1901 at the Eddystone Lighthouse in the English Channel. "Hosts of glittering objects, birds resplendent, as it were, in burnished gold, were fluttering in, or crossing at all angles, the brilliant revolving beams of light. Those which winged their way up the beams towards the lantern were innumerable, and resembled streaks of approaching light. These either struck the glass, or, recovering themselves, passed out of the ray ere the fatal focal point was reached. Those which simply crossed the rays were illumined for a moment only, and became mere spectres on passing into the gloom beyond. Some of those that struck fell like stones from

their violent contact with the glass ; while others glanced off more or less injured or stunned, to perish miserably in the surf below. Others, again, beat violently against the windows, in their wild efforts to reach the source of the all-fascinating light. Many of those that freed themselves from the dazzling streams of light came in sharp contact with the copper dome of the tower, making it resound like a drum, and then fell like flashes into the water below, followed slowly by a cloud of feathers, resembling a miniature shower of golden flakes. Finally, above and below the madding crowd in the illumined zone, great numbers of the migrants flitted around in all directions in the semi-darkness, and in almost weird contrast with the brilliant multitudes gyrating in the adjacent vistas of light. The babel of tongues, too, was a very striking feature. These were by no means the cries of enchantment, but of surprise and alarm : and they varied from the loud rattling notes of the Blackbird and the harsh angry 'churr' of the Mistle-Thrush to the faint and dainty twitter of the Gold-crest. Some Skylarks every now and then, under the impulse of excitement, no doubt, broke out into a few notes of song. Not a few strange voices were heard, some probably uttered by species with whose ordinary notes one was quite familiar : but migrants, especially Waders, have a travel-talk which is, as yet, an unknown tongue to most of us. Nor was it an easy matter promptly to assign a familiar utterance to its rightful throat, when heard under such highly peculiar conditions, and to an accompaniment supplied by the roar of the surf on the surrounding reefs." In other parts of the world similar scenes occur, but with different participants : Ticehurst, for instance, has recorded Cranes in hundreds round the lantern of a lighthouse in the Red Sea, the noise of the great birds being described as deafening.

If the weather conditions should become unfavourable for further flight, or if the birds are already tired or have lost their way, many of the migrants may come to rest about the lighthouse and be found there when daylight arrives. The same thing, of course, happens elsewhere than at light-stations, but would ordinarily pass unnoticed. On ships at sea, however, there are sometimes opportunities of observation of this kind, as is shown in the following description by Lynes (1909) of migrants crossing the Mediterranean which visited H.M.S. *Venus* in the afternoon and evening of the 29th April, 1906, when stormy weather was brewing : "At 4.30, when the ship was 50 miles from

the west end of Crete and 40 miles south of Cape Matapan, making about eleven knots to the westward, there commenced a regular rush of migrants. Some Yellow-bellied Wagtails, a Redstart, a Turtle-Dove, and a Whinchat appeared, the latter settled aft, the Wagtails were shyer and only followed in the wake of the ship, uttering vibrating chirps, the others flew around the ship. . . . At five o'clock two more Wood-Wrens came on board, and a party of seven Yellow-bellied Wagtails, which paddled nimbly about the quarter-deck searching for flies, which, unfortunately, did not exist. The next few minutes brought some Turtle-Doves, Whinchats, a Wheatear, and more Wagtails. The Turtle-Dove, I think, settled in the rigging, the Whinchats were quite tired out, and could only sit miserably hunched up, and next day two of them were found dead in the boats. About 5.30 Swallows started to arrive, and their numbers rapidly increased until Swallows were perched all over the ship in the most confiding way. They would crowd up together on the rim of a ventilator or a hatchway rail, heads and tails, as if to keep one another warm, and they did not mind us in the least when we walked up within a foot of them. They subsequently roosted all over the ship, several inside the chart-house, in the captain's cabin (half-deck) ; there must have been more than one hundred Swallows roosting altogether. Many were captured by the ship's company and liberated again. Although obviously very tired those Swallows that came under our particular notice did not seem to be wet, at any rate not drenched.

" After dinner some of the officers were walking up and down the quarter-deck, lighted by a single electric light underneath the awning ; a Swallow hovered over them and actually settled on the head of one, who was wearing a cap with a white cover on it, put its head under its scapulars, and went to sleep. The officer took his cap off and put it down on a grating ; the Swallow just raised its head for a moment, then tucked it away again and was at once asleep."

In spite of the frequency of nocturnal passages, a great deal of migration also takes place by day and may be observed under favourable circumstances. On the eastern seaboard of Great Britain it is no uncommon sight to see migrants coming in from the north-east in autumn, usually flying low over the sea in small parties. At that season bands of migrants may also be seen following the same coast-line in a southerly direction. But what one may see is usually only a very small fraction of the whole.

Diurnal movements on a great scale may be observed at islands and other places where the conditions are specially suitable for observation. Thus, on Heligoland the passage of many species takes place largely by day, and immense numbers of birds are involved. Some idea of this may be gained from a summary of the movements of Starlings (*Sturnus vulgaris*) visible from Heligoland, as described by Gätke, in the autumn of 1878. Early in June came a few old birds in worn plumage, birds which had probably remained unmated or had early lost their broods. On 20th June came the first great flights of young birds of the year, only a few weeks old, migrating by themselves in advance of their parents. These youngsters continued to pass till the end of the month to the extent of thousands daily. In early July the daily passage was estimated in tens of thousands, and on the 25th the movement closed with the passage of "immense multitudes." Two months followed, during which no Starlings, young or old, were to be seen. But on 22nd September old birds, now in fresh plumage, passed in flights of many hundreds. During October the flights increased to thousands, and on the 14th the movement reached a climax with "Starlings in hundreds of thousands." By the end of the month the great flights had ceased, but through November and even up till 18th December they continued to pass in frequent "daily flights of from forty to sixty individuals."

It was on Heligoland also, but under conditions that were not favourable for very large movements, that the present writer had an opportunity of witnessing the diurnal passage of Swallows (*Hirundo rustica*) on 20th September, 1908. All through the forenoon, as we sat in the autumn sunshine near the narrow northern apex of the island, the Swallows came in over the sea from the north-east in the teeth of a southerly gale. No large flocks were seen; but, on the other hand, scarcely a minute elapsed without the arrival of a fresh party of from half a dozen to a score of birds. They seemed to fly low over the sea, but rose as they approached us to the level of the cliff-tops. We could not make them out at any great distance, for the observer can find no worse background for small birds than grey, moving water. The stream was continuous and the direction unvarying, as far as we could judge. Each party rose to our level on the top of the north point, flew unhesitatingly along the western side of the island, and disappeared again at the south-western corner. Not one in a hundred quitted

this line or stopped to circle round; none seem inclined to break the journey so early in the day, in spite of the contrary elements. The whole was for us just a momentary peep at one of the countless tiny channels by which the bird-life of Northern Europe was then ebbing southward.

It will be of interest to supplement this description of a movement of Swallows in Northern Europe by an account of an incident in the migration of the same species which was witnessed by Lynes (1908) near Mombasa, British East Africa, on the 1st November, 1907: "About noon there flitted by two or three birds that looked very much like our English Swallow; and about 1.30 p.m. I became aware of an intermittent passage to the south-south-westward of small parties of the same species—five or six at a time. They were flying as in the Mediterranean I have so often seen them on migration, quite low, never more than 20 feet from the ground, and often just skimming over the tops of the long grass and bushes, but always pressing onwards in a steady business-like way, at the rate of about 25 miles an hour. At 2.30 p.m. I came upon a party of some fifty birds which had stopped travelling, and were circling low over a patch of grass catching flies." Up till this time the weather had been fine, but now a storm was imminent. "A banking up of the migratory stream resulted, fresh birds arriving continually from the north-north-east to swell the multitude, until the air was simply alive with Swallows wheeling around from the ground level to about 1000 feet high, evidently catching flies and making the most of their time. There must have been thousands within my field of vision." The weather cleared again, and by 4 p.m. the migrants "had melted away, leaving hardly a single bird in view, and in another five minutes not one European Swallow could be seen."

The greatest manifestation of migration which the present writer has witnessed, was in the neighbourhood of the German Ornithological Society's Observatory at Rossitten, lying at the south-eastern angle of the Baltic, almost midway along a narrow strip of land which separates a great lagoon from the sea. Here the conditions of observation were practically those of an island, and a great part of the movements took place by day. It was on the 2nd October, 1910, that we first saw a great movement of Hooded Crows (*Corvus cornix*), although on previous days these birds had been passing in smaller numbers. We betook ourselves to the seaward strip of sand stretching uninterruptedly as far

as we could see, north-eastward toward Russia and south-westward toward the Gulf of Danzig. On one side lay the quiet waters of the almost tideless sea ; on the other rose a line of low dunes over which the tops of the trees behind peeped here and there. The silence was complete but for the rhythmic murmur of gentle waves ; a slight breeze blew from the south-east, and the sky was lightly clouded at a great height, leaving the lower air extremely clear. The sun shone brightly, but the keen nip of October was in the air, showing that despite the glorious weather the autumn had entered on its final phase and winter was at hand. The steady progress of the Crow battalions told the same tale. Every minute or two a flock passed, flying steadily and quietly south-westward along the line of the shore at a height of from 100 to 300 feet. Hooded Crows were in the majority, Rooks numerous, and Jackdaws present in smaller numbers ; Rooks and Crows were generally in separate flocks, the Jackdaws accompanying the former. If we watched one flock pass overhead and recede in the distance, another was already passing before it had disappeared, and a third would be coming into view in the wake of the second. The line of the shore seemed to be followed with some exactness, for a bend a quarter of a mile from us caused the flocks to fly out over the sea for a few hundred yards before they wheeled to take the slightly altered direction. In size the flocks varied from thirty or forty to two or three hundred birds ; and we calculated that over two thousand birds passed every hour in an unbroken stream from early morning till after midday.

Next day was as beautiful as its predecessors, and the number of migrants greater than ever. Crows there were, as on the day before ; but the flocks were larger and more frequent, and continued to pass till well on in the afternoon. Some twenty or thirty thousand must have passed in the course of the day. It was not merely the vastness of the numbers that made the scene so impressive, but the fact that all these thousands were moving together with one accord, without great speed or appearance of haste, yet without halt or deviation, and still more noticeably without noise. The great army was advancing in column—a column of great length but of no appreciable frontage, and apparently without any parallel columns in its near neighbourhood. Not only was there a continual succession of these silent flocks of Hooded Crows, Rooks, and Jackdaws, but small song-birds were also on the move. Every few seconds

a small company of Larks or a little band of Finches passed us flying low down over the ground. Overhead, at a considerable altitude, were less frequent flocks of Wood-Pigeons, making more speed than most of the others. Here and there were a few birds of prey ; Kestrels were frequent, usually alone, sometimes three or four together ; and often, at our approach, some larger predatory bird would rise on broad wings from a meal provided by some weakling which had paid too high a price for the journey.

A narrow strip of barren sand bounded by expanses of desolate water made up the landscape that shimmered in the bright sunlight of that crisp autumn day. Nothing else was in sight but the vast flocks of birds, and every bird was moving onwards with the stream. It seemed to us that we were watching the ebb of the life of half a continent, an ebb which would leave the northern forests deserted and voiceless in the deathlike grip of the sub-arctic winter ; but we remembered that this same channel would in a few more months convey a contrary tide which would again fill these lands with the active bustle and cheerful sounds of feathered life.

Diurnal migration is also observed at times from ships at sea, and as an example of this may be quoted the following account of one of the movements observed in 1903 by Eagle Clarke from the Kentish Knock Lightship, moored in the North Sea off the estuary of the Thames and over twenty miles from the nearest land : " On the 10th October there was another considerable fall in temperature, and our thermometer registered 10 degrees lower than on any previous occasion since my residence in the lightship. This was followed on the 11th by the greatest diurnal movement of birds that I have ever witnessed. It set in at 8 a.m. with a marked passage of Starlings, Skylarks, and Tree-Sparrows. By midday it had assumed the nature of a 'rush,' which was maintained without a break until 4 p.m. It was a remarkable movement in many ways. Skylarks, Starlings, Chaffinches, and Tree-Sparrows not only passed westwards in continuous flocks, but many of these companies consisted of hundreds of individuals. So numerous were the Starlings composing some of these bands that when first observed in the distance they resembled dark clouds, and formed a conspicuous contrast to the leaden white-crested billows." Another remarkable movement was observed by him during his return journey from the lightship to Southend on 18th October. " During

the entire passage of four and a half hours—the distance travelled being close upon fifty miles—we were at first crossing the course of, and afterwards running parallel to, the flight of continuous flocks of Starlings and Skylarks and of fewer Chaffinches and Tree-Sparrows, all proceeding westwards, and all flying just above the surface of the calmest of seas and in the finest of weather. These flocks, especially those of the two first-named species, were never absent from view, and we must have encountered tens of thousands of these birds during the passage."

The experience of Lynes (1909) in the Mediterranean is that migration is to be observed at a distance from land only under abnormal conditions and this may perhaps be due to the birds flying at a greater height than when over the North Sea. Close to the coast, however, movements are frequently observed from ships during the proper season, and he describes one incident as follows : " During September, 1906, H.M.S. *Scylla* was at anchor off Alexandretta, in the Gulf of Iskanderun, at the very north-east corner of the Levant. For an hour or so during the forenoon (from memory I think it was about 10.30 to 11.30) for several days in succession, there was a considerable stream past the ship of White Storks, about eight or ten every hundred yards, steering a dead straight south-easterly course. They appeared to be flying in rather a leisurely way, between 10 and 50 feet above the surface of the water, and were obviously just crossing, by the shortest route, the mouth of the gulf, a distance across the water of some 25 miles. On reaching the far shore of the gulf (our side), they stayed their progress a little to assemble, wheeling around and mounting higher and higher, about five thousand strong—an impressive spectacle. Gradually they drew away, still circling round and still apparently rising, until, finally, perhaps half an hour after the last of the pack had passed the ship, the whole concourse of Storks became lost to view at an immense height over the hills in the direction of Aleppo."

To go farther afield for another example, and to obtain a glimpse of bird-migration as it exists in the Southern Hemisphere, the following description relating to the Argentine may be quoted from the works of Hudson : " I can almost say that when I first opened my eyes it was to the light of heaven and to the phenomenon of bird-migration—and the sight of it and the sound of it. For migration was then and there on a great, a tremendous scale and forced itself on the attention of everyone. . . .

The autumnal migration, which was always a more impressive spectacle than that of the spring, began in February, when the weather was still hot, and continued for three long months; for after the departure of all our own birds, the south Patagonian species that wintered with us or passed on their way to districts farther north would begin to come in. During all these three long months the sight and sound of passage birds was a thing of every day, of every hour, so long as the light lasted, and after dark from time to time the cries of the night travellers came to us from the sky—the weird laughter-like cry of Rails, the shrill confused whistling of a great flock of Whistling or Tree-Duck; and, most frequent of all, the beautiful trisyllabic alarm cry of the Upland Plover."

As a more detailed example the following description of the migration of the Military Starling, as observed in the Argentine, may be quoted from the same source: "On the approach of winter it would appear all over the plains, not travelling in the manner of other migrants, but feeding on the ground, probing the turf as Starlings do, the whole flock drifting northwards at the same time. The flock, often numbering many hundreds of birds, would spread itself out, showing a long front line of scarlet breasts all turned one way, while the birds farthest in the rear would be continually flying on to drop down in advance of those at the front, so that every two or three minutes a new front line would be formed, and in this way the entire body, or army, would be slowly but continuously progressing."

This chapter may be concluded with a reference to a form of migration very different from anything to be seen in northern latitudes, namely, the seasonal movements of Antarctic Penguins of various species. Although flightless, these birds perform notable journeys, and are regular in their comings and goings. The winter area of the Adélie Penguin (*Pygoscelis adeliæ*), for instance, is in the region of the floating floes of pack-ice some hundreds of miles north of the nesting grounds on the land of the Antarctic continent. The greater part of the journey is made by swimming, but on their arrival off their native coasts in spring there may still be some miles of unbroken sea-ice to be traversed between the open water and *terra firma*. Levick has given an account of the arrival of this species at the "rookeries" at Cape Adare, South Victoria Land (71° 14′ S., 170° 10′ E.). The first bird arrived towards the middle of October, and a week later the birds were coming in across

the sea-ice in such numbers that they formed a line stretching as far as the eye could see. "First would pass a string of them walking, then a dozen or so tobogganing. Suddenly those that walked would flop on their breasts and start tobogganing, and conversely strings of tobogganers would as suddenly pop up on to their feet and start walking." Soon the immigration reached its maximum. "Far away from the beach the line had become thicker, and was no longer in single file, the progress of the birds being slow and steady, but within half a mile or so from the beach excitement seemed to take possession of them, and they would break into a run, hastening over the remaining distance, the line now being a thin one with slight curves in it, each bird running with wide gait and outstretched flippers working in unison with its little legs." Within a month the colony was some three-quarters of a million strong.

The various accounts that have here been given or quoted of bird-migration in progress describe mere incidents in the living ebb and flow which continues to a greater or less extent over wide areas of the Earth's surface throughout the greater part of the four seasons of the year. The observer at a given spot, however favoured that place may be as regards its situation and the conditions for observation, does no more than obtain glimpses of the vast movements which take place. When he is able to record the passage, within the limited range of his vision and within the short space of a few hours, of tens and even hundreds of thousands of birds, some slight impression may be obtained of how inconceivably immense is the migration of millions and millions of birds during months at a time, and year after year, over thousands of miles of sea and land.

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CHAPTER IV

THE BEHAVIOUR OF MIGRATING BIRDS

"But as a troop of pedlars, from Cabool,
Cross underneath the Indian Caucasus,
That vast sky-neighbouring mountain of milk snow,
Winding so high, that, as they mount, they pass
Long flocks of travelling birds dead on the snow,
Chok'd by the air, and scarce can they themselves
Slake their parch'd throats with sugar'd mulberries——"

MATTHEW ARNOLD, "Sohrab and Rustum."

Altitude of flight—Velocity of flight—Duration of flight—Feeding—Gregariousness—Age and sex differences in migration—Migration and moulting—Nocturnal and diurnal flight—The attraction of lighthouses—Dangers of migration—Calling during flight.

THE altitude and the velocity of migration flight are two questions which have always been of great interest to students of the subject, and there has even been a tendency to invest them with the importance of major problems. This rather exaggerated position has in the main been due to the influence of the remarkable views expressed by Gätke, the ornithologist of Heligoland, whose enthusiasm seems to have outrun his critical faculty when he came to estimate numerically the performance of the migrants which he esteemed so greatly. Gätke held that the migration which he saw was but a fraction of the whole and unrepresentative at that, while the bulk of the migrants passed at altitudes which kept them far beyond human observation and with velocities unparalleled in the ordinary flight of birds: normal migration was, indeed, imagined by him to take place "with storm-like rapidity, at elevations level with the clouds." One must not be ungrateful to the man who has given the subject a mass of data of all sorts representing the work of a lifetime devoted to ornithological observation, but on these points his evidence, at best mainly circumstantial, can hardly be accepted in the light of the more exact knowledge now available. Despite early criticism by Whitlock, Helm, and other writers, Gätke's views on altitude and velocity may be said to have coloured the writings of a generation on the subject of migration, but there has in the meantime been built up by many other observers a substantial volume of precisely recorded facts

which clearly point to a very different and less startling conclusion. The evidence on both points has recently been summarised in very useful form by Meinertzhagen, who is himself responsible for many observations of a very valuable accuracy, and also by Lucanus.

Altitude

Gätke's view that birds usually travelled at great altitudes, perhaps 20,000 feet (and he believed that they could go to 40,000 feet !), was largely based on three purely theoretical assumptions. One was that already mentioned, namely that the migration which he saw was only a fraction of what took place even by day over Heligoland, and that the remainder must, therefore, be beyond the range of his vision. Another was that in the rarefied atmosphere at high levels the migrants would be able to make better speed owing to decreased air resistance : this is a physical fallacy which scarcely needs discussion in these days when the facts of aviation are so familiar. The third was that a high altitude is necessary, during sea-crossings especially, so that landmarks may be kept in view, and this may be considered more fully. Meinertzhagen has pointed out that an elevation of no more than 5000 feet would in any case suffice for this purpose in almost all parts of Europe, Asia, and Africa, and that on the other hand there are cases elsewhere in which the condition could not be fulfilled except at altitudes entirely impossible. Moreover, there is every reason to suppose that birds are not wholly dependent on the visibility of landmarks for finding their way, mysterious as the fact may be. It is admitted even by Gätke, for instance, that some birds cross the sea at very low levels, and Levick has pointed out that the Adélie Penguin finds its way for hundreds of miles through trackless sea and for many miles over featureless ice-floe in spite of the fact that even when standing upright on the ice its horizon must be limited to about a mile. During nocturnal flight, moreover, migrants must frequently be without the assistance, whatever their altitude, of the sight of distant objects. The general question as to how birds find their way on migration is, however, a matter for discussion at a later stage in this book.

Gätke based his views on the subject to a lesser extent upon his own observation of migration over Heligoland. He gave various instances of birds seen flying over at great heights, and of birds ascending until they disappeared from

his view in a clear sky. One can only say that the figures he deduced from these observations cannot be accepted without great reserve. He admitted that much migration at low levels does take place, although as already stated he considered this to be abnormal, and that a few species are habitually low fliers : of these he mentioned especially the Hooded Crow (*Corvus cornix*), the Starling (*Sturnus vulgaris*), and the Skylark (*Alauda arvensis*), and it is perhaps significant that these species are numerically among the most important of the migrants over Heligoland.

To justify rejection of Gätke's observational deductions, as distinct from his purely theoretical inferences, Lucanus made some experiments on the altitudes at which different birds could be seen from the ground : the figures arrived at may be quoted here as they may perhaps serve as a guide to the rough estimation of altitudes when the observer has no means of measurement available. Birds stuffed in the attitude of flight were suspended from a captive balloon in such a way that they could be seen from the ground against the sky. It was found that the outline of a Sparrow-Hawk (*Accipiter nisus*) was distinguishable at about 800 feet, that the bird was clearly visible as a spot at about 2100 feet, and disappeared from view at about 2800 feet. The corresponding figures for the Rook (*Corvus frugilegus*) were about 1000, 2600, and 3300 feet. Yet Gätke spoke of seeing Sparrow-Hawks at 10,000 feet and Rooks at 15,000 feet ! The outlines of a Buzzard (*Buteo buteo*) and a Lammergeier (*Gypaëtus barbatus*) were visible up to about 2000 and 3000 feet respectively, and, by calculation, these birds would become invisible at 5000 and 6500 feet.

The same writer has used as an argument against flight at high altitudes the results of the well-known physiological experiments made by Bert on the effects upon birds of artificially produced conditions of low atmospheric pressure, low temperature, and low carbon dioxide value. It seems, however, unnecessary here to pursue the theoretical aspects of the question further, in view of the availability of a considerable body of recent factual evidence of a reliable kind.

Throughout ornithological literature are to be found only a few scattered records of birds, migrating and otherwise, observed at very great altitudes. Records of birds passing over at " a great height " are perhaps common enough, but expressions of this kind may imply no more than 2000 or 3000 feet. That some birds which cross high mountain ranges during migration must attain a great altitude above

sea-level is of course obvious. Many migrants cross the Himalayas, in which the lowest passes are some 18,000 feet above sea-level, as well as other great mountain ranges, and it is to this that the quotation at the head of this chapter is appropriate. Alpine climbers will know, too, of a pass over the Mont Blanc range, the Col des Hirondelles (11,370 feet), which takes its name from an incident similar to that described by the poet. But here the question of altitude is being considered in terms of height above the earth's surface at the particular point.

The experience of such observers as Eagle Clarke on the Eddystone lighthouse, Patten on the Irish coast, Thienemann on the Baltic coast of Germany, and Meinertzhagen in British East Africa and elsewhere, is all to the effect that migrants commonly travel at altitudes of from a very few feet to a few hundred feet above the surface of the sea or land. Lynes notes that migrants under ordinary circumstances are very little seen from on board ship in the Mediterranean except within a few miles of the coast, but he does not claim that any immense altitude during the mid-sea journey is necessary to account for this.

During the Great War of 1914–18 a very favourable opportunity occurred for making observations on any bird-life which might be found at great altitudes. Day by day in many parts of the world hundreds of military airmen were engaged in patrolling different levels of the air under circumstances which involved keeping a sharp look out in all directions. From the ground, also, continual anti-aircraft observation with telescopes was taking place. The experience of officers of the Royal Air Force has been collected by Ingram and by Meinertzhagen, and that of German airmen by Weigold, while earlier records have been given by Lucanus. From all the mass of available data from this and other sources Meinertzhagen (1920) extracts only thirty-six records of migrating birds observed at greater elevations than 5000 feet, of which only seven were above 8500 feet: Cranes (*Megalornis grus*) at 15,000 feet on one occasion represented the extreme limit, while Lapwings (*Vanellus vanellus*) were the most frequently recorded birds at high levels, 8500 feet being their greatest altitude. The experience of airmen was that the almost total absence of bird-life above 3000 feet is remarkable, and that even at that height few birds are encountered even during the principal seasons of migration. Lucanus similarly concludes that most flight takes place below 1300 feet, and that flight above 3300 feet

is exceptional. It may be added that it is now well known that birds are generally very little alarmed by aircraft, and that the paucity of records at high levels cannot be explained away on any theory of avoidance.

So far mention has not been made of nocturnal migration, about which it is naturally difficult to say much on the score of altitude. Estimates based on the audibility of cries heard overhead are unsatisfactory, and visual evidence is confined to a few observations, such as those made in America by Scott, Chapman, and Carpenter, of birds seen through telescopes against the face of the moon : the two first observers mentioned made some high estimates, but there was admittedly a wide margin in their calculations. Similar observations made in Germany by Spill are quoted and adversely criticised by Lucanus. The fact that migrants are attracted by lighthouses is not helpful, as this only occurs during thick weather. On the whole there is no evidence that birds fly at any greater altitude during the night than during the day, although it is not improbable that there may be less flight at very low levels owing to the danger of striking obstacles.

Speaking generally, and admitting the desirability of further records of an exact nature, there would seem to be justification for Meinertzhagen's findings, based on his review of the available evidence. He concludes that birds met with above 5000 feet are the exception and not the rule, and that the bulk of migration flight is conducted below 3000 feet whether by day or by night. In the case of some species at all times, and of all birds under adverse weather conditions, the altitude of migration flight is very small. One must, however, guard against the conclusion that birds cannot live or fly at high altitudes. It has already been made clear that the question here discussed relates to height above the earth's surface at the particular point and not to height above sea-level, while it is upon the latter that atmospheric conditions mainly depend. In some parts of the world migration necessarily takes place at a great altitude relatively to sea-level, and many birds ordinarily live, in the Himalayas for instance, at altitudes of more than 15,000 feet.

Velocity

In the matter of the velocity of migration flight Gätke's views were based on theory to an even greater extent than in the altitude question. His line of argument was to make an assumption that a certain distance is necessarily

covered in a single flight, and that this flight must be accomplished within a certain time: from this he deduced extraordinary figures for velocity. For instance, he argued that the Bluethroat (*Luscinia svecica*) leaves its African winter quarters at dusk and reaches Heligoland at dawn, covering some twenty-seven degrees of latitude in nine hours. This means that this tiny bird is credited with a sustained velocity of over 200 English miles per hour. The sole ground for the assumption that the distance is covered in a single flight is that the species is seldom observed in the intervening countries. This has been denied by continental observers, but in any event the argument can be answered in Gätke's own words: "To control a district of about four miles in diameter, and presenting the varied features of wood, moor, corn-fields, meadows, and water, is in itself almost an impossibility. How would one be able to determine day by day what different species have occurred in such different localities? The case of Heligoland is, of course, different, for here we may say without hesitation that literally not a single bird escapes observation." It is indeed a commonplace that resting migrants of small Passerine species are very apt to escape observation except under such favourable conditions as are afforded by small islands possessing little cover.

In a similar manner Gätke argued that the American Golden Plover (*Charadrius dominicus*) flies from Labrador to Brazil in autumn without a stop, and that fifteen hours is the longest time that can be allowed for a single flight. This gave a velocity of nearly 250 English miles per hour. Again, he stated that on autumn days the flocks of Hooded Crows (*Corvus cornix*) begin to pass westwards over Heligoland about 8 a.m., while Cordeaux informed him that they reached the English coast about 11 a.m. This gave a speed of about 125 English miles per hour (according to Gätke's slightly excessive estimate of the distance), and it is astonishing that anyone who has witnessed the deliberate flight of this species on migration should accept such a figure as within the bounds of possibility. It is now believed that the birds passing over Heligoland do not keep this direction of flight, and they cannot be the same birds as are seen arriving on the Yorkshire coast.

The only case in which Gätke appears to have estimated velocity by actual observation is that of Plovers, Curlew, and the like, which he timed as covering the 22,000 feet between the island and an oyster-bed to the eastward in

the space of 60 seconds, or at the rate of 250 English miles per hour. In the light of other observations one can only say that either his judgment or his methods must have been seriously at fault.

Gätke relied, also, on the alleged achievements of Homing Pigeons, and he quotes from Yarrell a case of one which flew from Ghent to Rouen at a speed of over 100 English m.p.h. Homing Pigeons, according to Riviere, have been reliably recorded as achieving such speeds as 82 m.p.h. over an 80 miles course, 65 m.p.h. over 366 miles, and 57 m.p.h. over 601 miles : these speeds, however, do not allow for wind, and when the data for the calculations are available it is found that the "air speed" falls between 30 and 45 m.p.h.

One may well doubt the authenticity of a record of a Swallow (*Hirundo rustica*) which is said to have been taken from Roubaix to Paris and to have flown the return journey of 160 English miles in an hour and a half, that is, at 106 m.p.h. This case found its way into ornithological literature in this country from a newspaper account in 1889 (*nec* 1887) and has been repeatedly quoted with varying degrees of credulity or scepticism : the distances between the places named is not even correctly given, and should be about 135 miles, making 90 m.p.h. Similarly in Germany, according to Lucanus, attention has been given to the case of a Swallow which was reported in a Belgian magazine of 1896 to have done the 146 miles from Compiègne to Antwerp in 1 hour 8 minutes, or practically 130 m.p.h. Experiments made by Loos with Swallows, on the other hand, have shown that the birds take several hours to return to their nests if removed to quite short distances. The best performance was 20 miles in $2\frac{1}{2}$ hours, a figure which obviously gives no true indication of the bird's powers of flight in a direct line : another took as much as 8 hours to return from a very slightly greater distance.

It is interesting to compare with the speculations of Gätke the conclusions arrived at by a modern German ornithologist as the result of careful measurements. Thienemann records the following speeds, among others, observed in the case of birds on autumn migration at Rossitten on the Baltic coast : Hooded Crow (*Corvus cornix*) 31 m.p.h. ; Jackdaw (*Colœus monedula*), 38·2 m.p.h. ; Starling (*Sturnus vulgaris*), 46 m.p.h. ; Finches, 32·6 m.p.h. ; and Crossbills (*Loxia curvirostra*), 37·1 m.p.h. The figures represent the average of observations made of flight over a measured stretch of

500 metres: they are corrected for the influence of wind, the strength and angle of which was noted in each case.

Lynes has recorded a measured speed of 57 m.p.h. in the case of Quail on passage over the Mediterranean.

During the war Meinertzhagen (1921) had opportunities of making a number of accurate observations on migrants in different parts of the world, usually employing the instruments of the anti-aircraft equipment by way of practice for the men in charge of them. The following may be cited as examples:

	M.P.H.	
Rook (*Corvus frugilegus*).	39	Side wind.
Red-throated Pipit (*Anthus cervinus*).	26·5	Wind calm.
Wagtails.	30·1	Slight following wind.
Swallow (*Hirundo rustica*).	37·75	Wind calm.
Roller (*Coracias garrulus*).	38·7	Slight head wind.
Kestrel (*Falco tinnunculus*).	40·5	Wind calm.
Geese.	50·25	Head wind of 9 m.p.h.
Lapwing (*Vanellus vanellus*).	42	Side wind.

His records also include a large number relating to birds which were not at the time on migration, and of these the following are examples:

	M.P.H.	
Raven (*Corvus corax*).	32–39·5	Wind calm.
Starling (*Sturnus vulgaris*).	43–49	Wind calm.
Common Bunting (*Emberiza calandra*).	29·5	—
Lanner Falcon (*Falco biarmicus*).	48	—
Marsh-Harrier (*Circus æruginosus*).	31, 36, 37·5	Wind calm in first two cases.
Lammergeier (*Gypaëtus barbatus*).	79·25	(gliding down at 12° to the horizontal; side wind).
Pelican (*Pelecanus* sp.).	51	Side wind.
Ducks.	51–59	Wind calm.
Teal (*Anas crecca*)—leisurely.	44	—
Houbara Bustard (*Chlamydotis undulata*).	42·25	Wind calm.
Stock-Dove (*Columba œnas*).	42·25	Strong head wind.
Sandgrouse (*Pterocles orientalis*).	43·75	Slight head wind.
Sandgrouse (*P. senegallus*).	47·5	Wind calm.
Turtle-Dove (*Streptopelia turtur*).	37	—
Geoffroy's Plover (*Charadrius geoffroyi*).	34	Wind calm.
Kentish Plover (*C. alexandrinus*).	34	Wind calm.
Dotterel (*C. morinellus*).	45, 50·5	Side wind.
Caspian Plover (*C. asiaticus*).	47	Strong side wind.
Lapwing (*Vanellus vanellus*).	37	Head wind of 12 m.p.h.
Little Stint (*Calidris minuta*).	49	Wind calm.
Terek Sandpiper (*Terekia cinerea*).	48–51	Wind calm.
Greenshank (*Tringa nebularia*).	46, 49	Wind calm.
Marsh-Sandpiper (*T. stagnatilis*).	48, 51, 51·5	Wind calm.
Oyster-Catcher (*Hæmatopus ostralegus*).	45–49	Wind calm.
Curlew (*Numenius arquata*).	42–48·25	Wind calm.
Whimbrel (*N. phæopus*).	43–52	Wind calm.

Meinertzhagen (1921) has also collected observations made by pilots of the Royal Air Force who had observed the speed indicators of their machines while keeping level with the birds. Only two of these records refer definitely to birds actually on migration: White Storks (*Ciconia ciconia*) were encountered migrating at 48 m.p.h. at 4200 feet, and Mallard (*Anas platyrhyncha*) migrating at 50 m.p.h. Other speeds recorded are as follows: Rook, 45; Gannet (*Sula bassana*), 48; Geese, 55; and Lapwing, 40–45 m.p.h. Greater velocities were recorded in three instances. Golden Plover (*Charadrius apricarius*) when pressed by a pursuing aeroplane accomplished 60 m.p.h.; Swifts (*Apus apus*) feeding at a height of 6000 feet above Mosul easily passed and circled round an aeroplane doing 68 m.p.h.; and a Lammergeier made 110 m.p.h. while "nose-diving" to escape an aeroplane.

Reference has already been made to corrections for wind in the case of measurements of velocity taken from the ground. The speed of a bird on the wing relative to the ground is of course affected by the speed and direction of movement of the body of air in which the flight is taking place. In calm weather "ground speed" and "air speed" are one and the same, but otherwise it is the "air speed" which is the true measure of the bird's capacity and the ground measurements must be corrected accordingly. The speed of a bird as measured from an aeroplane flying near it and in the same direction is of course its true "air speed," as the body of air is moving to the same extent relatively to each of them. The figures given in the previous paragraph are therefore all "air speeds."

From a review of his own and other observations, Meinertzhagen concludes that birds have an ordinary speed and an accelerated speed—used when pursuing prey, when in danger, or when mating—which can be maintained over a short distance: some species of birds are capable of a greater degree of acceleration than others.

He concludes, further, that it is the ordinary speed which is used on migration, and with this finding probably everyone who has ever seen migration in progress will agree. There is indeed no reliable evidence in favour of the view that during migration any exceptional velocity is achieved or indeed that any attempt at acceleration is usually made. The average ordinary velocities, used on migration, he puts as follows for different kinds of birds:

Crows	31–45 m.p.h.
Starling	38–49 m.p.h.
Smaller Passeres	20–37 m.p.h.
Falcons	40–48 m.p.h.
Geese	42–55 m.p.h.
Ducks	44–59 m.p.h.
Sandgrouse	43–47 m.p.h.
Waders	34–51, but mostly 40–51 m.p.h.

Length and duration of flight

Leaving aside wild speculations based on mere hypothetical assumptions, the definite evidence as to the length and duration of migration flight may next be briefly considered.

In the case of many species which have widely separated seasonal areas one can at least state certain minimum figures for the total lengths of the journeys which must be performed. Thus the Arctic Tern (*Sterna macrura*) is not found in summer south of about 40° N. lat., and not so far south on the European side of the Atlantic : in our winter the species ranges as far as 74° S. lat., so that journeys of at least 6000 English miles must be made. Similarly, the Curlew-Sandpiper (*Calidris ferruginea*) must travel at least as far from its breeding grounds on the Arctic tundras to the temperate regions of the Southern Hemisphere which it visits during the rest of the year. That some individual birds go from one extreme of their specific range to the other and so travel about 11,000 miles is quite probable.

In other cases deductions are not so readily made from the seasonal ranges of the species, or information as to these may be incomplete. Without evidence as to the precise winter quarters of birds from a particular part of the summer range of the species, speculation is dangerous. Such evidence, however, is beginning to become available from the marking of birds, and there are definite records, to be dealt with more fully later in the book, of marked birds of various kinds performing the journey of some 6000 miles from Northern Europe to South Africa.

The cases so far considered are of course extreme examples, and from these there is every gradation down to journeys of a few hundred miles and mere local movements from high ground to neighbouring valleys.

From such knowledge as is available as to the dates of arrival and departure of long-distance migrants in their

winter quarters some inferences may be drawn as to the time occupied by the journeys. In most cases, however, calculations of this kind involve several hypothetical factors, and it accordingly seems desirable to regard this as a branch of the subject in which further knowledge is required before useful conclusions can be drawn.

The distance covered in a single flight is, as a rule, probably not very great, but here again one has to rely mainly on circumstantial evidence. The rate of spread of immigratory species does not throw much light on the performance of individual birds. The Swallow is about a fortnight later in reaching Scotland than in reaching the south of England, for instance, but it does not follow that it is the same birds which have gradually moved on 300 miles in this period : indeed the contrary is almost certainly the case. Similarly, the rate of spread of summer immigrants in North America is given by Cooke as averaging from 20 to 130 miles a day according to species.

Better inferences may be drawn from the known velocities of various species and the probable duration of continuous flight. Most observers seem to be agreed that migration is by no means maintained for the whole of a day or night. In the case of diurnal migration it is certainly true that at many different places movement is commonly confined to the earlier part of the day. Assuming a flight of from six to eight hours, and a speed of from 30 to 40 m.p.h., one arrives at figures ranging from 180 to 320 miles. In many cases, especially under bad conditions, the distances covered are not improbably much less. Some further evidence has recently been obtained by the marking method and will be discussed at a later stage.

As to the maximum distances that may on occasion be covered in a single flight there is little evidence except such as can be deduced from the dimensions of stretches of uninterrupted sea which migrants are known to cross. The passage of the northern part of the North Sea involves a flight of from 220 English miles (Norway to the Shetland Isles) to 400 miles (Norway to the Yorkshire coast). The Mediterranean crossings probably do not exceed some 450 miles at the most, and many are much shorter. The Gulf of Mexico is stated by Cooke to be crossed in directions which involve flights of from 500 to 700 miles. Unless the few small intervening islands be used, migrants to and from New Zealand must necessarily make single flights of from 600 to 900 miles in length.

According to Cooke the American Golden Plover (*Charadrius dominicus dominicus*) on its autumn migration frequently makes an uninterrupted flight of 2400 miles from Nova Scotia to South America, although resting-places are available. Also, according to Cooke and to Henshaw, its near relative, the Asiatic (or Pacific) Golden Plover (*C. d. fulvus*) flies direct from Alaska to Hawaii, a stretch of some 2000 miles offering no possibility of rest near the direct route.

That the Atlantic Ocean is frequently crossed is shown by the numerous records of North American birds on the western sea-board of Europe, and also of European birds on the eastern coast of America. The commonest American visitors on this side are Limicoline species from high latitudes, and these probably come by way of Greenland and Iceland, a journey not necessarily involving any single flight of as much as 300 miles. There are other species, however, which are unlikely to take so northerly a route—and as unlikely, it would seem, to come by way of Alaska and Siberia as Lucanus suggests—and their occasional appearances can thus be explained only by admitting trans-oceanic flight or postulating an "assisted passage." The distance from Newfoundland to Ireland is about 1750 miles, but by way of the Azores, on a more southerly route, the passage could be made without any single flight of as much as 1000 miles. Farther south still, Africa and South America are at one point only some 1600 miles apart.

Land birds have occasionally been recorded as resting on the surface of the sea, but these were probably exhausted individuals. It would in any case scarcely be possible except in the calmest of weather, and there is no reason to believe that the occurrence is other than exceptional. With sea-fowl and even with other aquatic birds the case may obviously be very different, and the following incident described by Lynes may be quoted as an example: "This happened on March 27th, 1897. H.M.S. *Scylla* was steaming from Malta to Port Said, and, being somewhere to the north-westward of Alexandria at 5 p.m. on this calm and sunny afternoon, there came a hail from the man at the masthead of 'Shoal on the starboard bow.' Knowing that the ship was in the middle of the Levant, and that the nearest land was quite 100 miles away, this report was naturally received on the bridge with a certain amount of suspicion. However, as the ship continued her course, it became evident to those on the bridge that there was indeed a shining white patch about an acre in extent on the bearing

indicated. The ship's course was altered for this patch, which turned out to be a compact flock of about 500 Pelicans, seated on the water, apparently enjoying a rest. These birds were presumably on their northward migration, and since weather conditions were entirely favourable to migratory passage, the inference seems to be that Pelicans normally have the habit of resting on the water during their passage."

Of the intervals between stages of a migration journey it is not possible to say much. On a place like Heligoland birds usually remain but a single day, arriving one night and leaving the next. Where the surroundings are more favourable for a sojourn, however, it may well be that several days are spent, and observations on Limicoline birds on the coast in autumn lead one to believe that particular parties indeed remain stationary for some little time before continuing their migration. The necessity for feeding must be even greater than usual during migration, in view of the immense expenditure of energy in flight. Birds killed on migration are generally found to have completely empty stomachs and intestines, and the inference is that both food and rest must be necessary before a further stage can be embarked upon. In observing Limicoline migrants on the Dutch coast in autumn, Bonhote noted that new arrivals were usually thin and that they became very fat after some days of rest before resuming their journey. He concluded that a single flight or continuous series of flights of no inconsiderable length must be made to have this great effect, and that the journey was therefore made in long stages with intervals of several days between each.

The difference between the autumn migration, often apparently leisurely in its progress, and the spring migration, when the urge towards the destination seems to be stronger, has already been mentioned.

Gregariousness

Gregariousness is a characteristic feature of the migration of the majority of species, including many of those which show in special degree the tendency to be solitary in the breeding season and hostile to all intruders on the chosen territory of the pair. Many species customarily migrate in large flocks, and the process of concentration into these is one of the most familiar aspects of migration. Birds-of-prey and Owls are among the best examples of habitually non-

gregarious migrants, although even in these cases small parties may at times be formed. Cuckoos (*Cuculus canorus*) also are solitary migrants.

The flocks formed by gregarious migrants vary greatly in size. Geese, for instance, often migrate in what appear to be family parties. Many small Passerine and Limicoline species commonly travel in small bands of, say, from twenty to fifty birds, but larger flocks may be formed. Flocks of hundreds or more are common in the case of the Hooded Crow, the Starling, and other birds. Storks and Cranes are sometimes seen in thousands. No general rule can be stated, but some species certainly seem to show a greater tendency than others, equally or even more abundant, to form very large flocks. On migration different species often fly in company in mixed flocks, as in the case of Rooks and Jackdaws, or of Swallows and House-Martins (*Delichon urbica*).

Passing mention may be made of the flight formations which are characteristic of some birds which fly in company. The wedge formation often assumed, on migration and otherwise, by such birds as Geese, Ducks, and Cranes is well known. The flocks of other species, such as Crows, Starlings, and Storks, usually seem to be without special form or order.

Age and sex differences in migration

Differences in migration behaviour related to age and sex may also be referred to here. In a great many cases the young of the year are the first to leave, the adults often being delayed until they have completed their seasonal moult. A few old birds, probably those which have not bred or which have been unsuccessful in their nesting, usually migrate early.

Gätke was strongly of opinion that what has just been stated held good as a general rule for almost all the species which came under his observation on Heligoland, but this would seem to be an over-statement of the case. To some extent he is supported by Gurney, whose opinion is based on many years of observation on the Norfolk coast. On the other hand, such writers as Brewster and Allen have stated that among North American birds it is the practically invariable rule for the old birds to migrate first in autumn ; but it is not quite clear whether this means that a few old birds migrate early, or that the bulk of the old birds are earlier than the bulk of the young.

It would seem, in any event, that no general rule can be laid down. With some kinds of birds old and young apparently migrate at the same time.

In the special case of the Cuckoo (*Cuculus canorus*) the adults are very early in their departure and leave in advance of their young, which are reared by foster-parents of other species.

Gätke held that adult males tended to be later in their autumn migration than the females, but this view seems to lack confirmation. Certainly the adult males of many species begin to arrive in the breeding area in spring some little time before the females, a point clearly brought out, for example, in Howard's studies of the Warblers and by the exact methods used by the Alexanders in observing and recording the arrivals of summer visitors.

Among Limicoline birds nesting in the far north, where the summer is extremely short, courtship activities sometimes take place during halts on the spring migration.

Migration and moulting

The question of migration and moult is one about which further information is required, but the evidence which exists shows clearly that the relationship is not a constant one such as could be expressed in a general statement applicable to all birds, and also that it may vary even within the species. The existing knowledge as to moulting is in itself far from complete, but for present purposes it will suffice to state that it is common for birds to have two moults, complete or partial, in the year, occurring in autumn and in spring, respectively. The immediate question is the relation between the times of these moults and the times of migration.

Rintoul and Baxter have noted the frequent occurrence at British lighthouses, in autumn and in spring, of migrating Passerine birds in a state of moult, especially as to the body feathers. Ticehurst, dealing with similar and additional data, concludes that the vast majority of Passerine birds moult before migrating: exceptions include the Swallow and House-Martin. At the same time he notes that individuals of practically every species may be found in which the moult is not finished at the time of migration, such unfinished moult being nearly always confined to the body plumage, quite exceptional in the tail, and practically never shown in the wings. Among non-Passerine birds there are

notable differences as between one kind and another. Some usually moult before the autumn migration; others, like the Swift and both adult and young Cuckoos, apparently do not moult until the winter quarters are reached; Terns frequently moult during their leisurely southward passage.

Observations in this regard have been made by Jackson on certain species of Waders in which the wide separation of the summer and winter ranges enables it to be definitely stated that they are on passage if found in the intervening area. The conclusion is that adults may begin the moult of the body plumage in their breeding grounds or on southward migration, but only rarely that of the wing quills: in the winter quarters the moult of the wing quills and usually of the tail quills takes place, and that of the body feathers is completed. The young birds, as a rule, do not begin the post-juvenile moult before leaving the breeding grounds, but a greater degree of moulting during passage seems sometimes to occur than in the case of adults. The spring moult begins, and is in many cases completed, in the winter quarters.

Nocturnal migration

The fact that a great part of migration takes place by night is of much interest, considering that most birds are diurnal in their ordinary life, and that many of them usually seem helpless in the dark. At different times and different places, however, the same species of birds migrate both by night and by day, and it would perhaps be rash to describe any of them as either purely nocturnal or purely diurnal migrants. Of birds which seem to travel nearly always by day, the members of the Crow family may be mentioned as examples.

It has been suggested that nocturnal migration may serve the purpose of protecting from birds of prey the smaller species of travellers, forced to make sustained flights far from cover and subject to great exhaustion. It must be noted, however, that large species, to which this remark is inapplicable, are also numbered among the nocturnal migrants. A more important point is probably the necessity for feeding during the day, and it may be said that in many cases a long diurnal flight would necessarily involve a stretch of two nights and a day with little sustenance, just when the requirements must obviously be very great.

Speaking of North American migrants, Brewster many years ago made some interesting generalisations on this

subject. He held that timid, sedentary, or feeble-winged birds migrate by night, while bold, restless, strong-winged birds migrate chiefly, or very freely, by day. The latter, being accustomed to seek their food in open situations are indifferent to concealment, and being able to accomplish long distances rapidly they can ordinarily spare time to stop for food by the way : but when crossing wide stretches of water or of desert land they tend to fly by night. Birds of easy and tireless wing, which habitually feed in the air or over very extensive areas—Swallows, Swifts, Hawks—fly exclusively by day, often obtaining their food as they go. Many wading and swimming birds appeared to him to migrate indifferently by day or night, being accustomed to feed at all hours and not accustomed to seek safety in concealment. He added that certain Ducks and other birds, accustomed to dive when in danger, travelled by day along the coasts, but by night if passing overland.

These generalisations of Brewster seem to fit the facts in large measure if applied also to European species. It will be noted that they combine the two factors of safety and of food requirements.

The attraction which the lantern beams of light-stations have for nocturnal migrants is another interesting point, and some reference to this has already been made. This is less noticeable in clear weather, but when the atmosphere is full of moisture the rays have a dazzling effect which lures the birds to what is often their doom : sometimes they fly straight up the beam and dash themselves headlong against the glass, and at others they are kept fluttering round like moths at a candle. It is only white lights which have this effect, stations with red or green lights apparently not attracting the birds. This is no mere accident of geographical position, for Eagle Clarke quotes the experience of the Galloper Lightship, which was changed from white to red and then ceased to attract the birds which formerly came in plenty.

Lighthouses and lightships have thus added a new danger to migration, already perilous enough. Through loss of direction, exhaustion, sudden storms, and like causes, vast numbers of birds must annually perish at sea as part of the price which the race pays for the advantage of migration. The predatory species, too, levy toll on their weaker brethren, and all have to run the gauntlet of human enemies in the countries where halt is made on the journey.

Calling

When birds migrate by night, especially, there is often a great deal of calling. Eagle Clarke has remarked, in this regard, that the notes used by Limicoline birds while on migration are different from their ordinary cries, and are in a language which observers are still unable to recognise. Tyler has recorded a similar fact in the case of certain North American migrants. Birds have sometimes been recorded as singing while actually on migration, and an instance of this was quoted in the previous chapter: Baxter and Rintoul have also recorded Willow-Warblers (*Phylloscopus trochilus*) as singing at a lighthouse lantern. That some birds sing at times when stopping on migration, especially in spring, is shown by observations of Alexander, of Baxter, and Rintoul, and of others. Tulloch has recorded the singing of the Blackcap (*Sylvia atricapilla*) in May in the Shetland Isles, where the species is purely a bird of passage. Mention may also be made of the observation of Mouritz that Willow-Warblers, apparently just arrived, were heard singing feebly in October in the Congo.

Calling may at times serve the purpose of keeping the flocks together at night, but Hudson relates of Bartram's Sandpiper or "Upland Plover" (*Bartramia longicauda*) that it cries incessantly on migration by day and by night, although it is a solitary traveller. The cry is the alarm note—as if the urge to migrate was akin to fear. "Lying awake in bed, I would listen by the hour to that sound coming to me from the sky, mellowed and made beautiful by distance and the profound silence of the moonlit world. . . . It was the sense of mystery it conveyed which so attracted and impressed me—the mystery of that delicate, frail, beautiful being, travelling in the sky, alone, day and night, crying aloud at intervals as if moved by some powerful emotion, beating the air with its wings, its beak pointing like the needle of the compass to the north, flying, speeding on its seven-thousand-mile flight to its nesting home in another hemisphere."

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CHAPTER V

MIGRATION ROUTES AND FLIGHT-LINES

" Sister, my sister, O fleet sweet swallow,
Thy way is long to the sun and the south."

SWINBURNE, " Itylus."

Terminology—Evidence for the existence of definite routes—Migration in concentrated paths and on a wide front—Principal European routes—Trans-Alpine migration—North American routes—Differences between autumn and spring movements—To what extent are routes constant ?—Effect of extensions of range—The flight-lines of individual birds—Do they follow definite paths ?—Two extreme views, and a compromise—Possible evolutionary significance of routes.

THE much used, and often abused, term " migration route " covers two distinct ideas, which it is desirable clearly to distinguish. In the first place there are the general directions constantly followed by the principal movements. In the second place there are the actual lines of flight of individual birds. For the sake of clarity, the term " route " will be restricted in this chapter to the former meaning, the term " flight-line " being employed for the latter.

It is to be noted that whereas the route is largely a theoretical concept, the flight-line is a matter of simple fact. Yet it so happens that nearly all the available evidence has to do with routes, for it is only the directions of general movements which can be observed : flight-lines, except over short stretches within a single observer's range of vision, can as a rule only be inferred.

With regard to routes, it is beyond doubt that certain general directions of flight are constantly followed by regular migrants, and also that migration flight is in places more or less restricted to definite paths which follow coast-lines or other geographical features. Mention has already been made, for example, of the general directions of the main movements in the British area, and of the fact that these movements very largely follow the coasts of our islands.

Narrow paths may at times be followed even by trans-continental movements, as is shown by such evidence as

the following description given by Hudson of the migration of the Buff-breasted Sandpiper (*Tryngites subruficollis*) in the southern autumn, in the Argentine, towards its Arctic breeding grounds : " The birds appeared in flocks of about one to two or three hundred, flying low and very swiftly due north, flock succeeding flock at intervals of about ten or twelve minutes, and this migration continued for three days, or, at all events, three days from the first day I saw them, at a spot about two miles from my home. I was amazed at their numbers, and it was a puzzle to me then, and has been ever since, that a species thinly distributed over the immense area of the Argentine pampas and Patagonia could keep to that one line of travel over that uniform green, sea-like country. For, outside of that line, not one bird of the kind could be seen ; yet they kept so strictly to it that I sat each day for hours on my horse watching them pass, each flock first appearing as a faint buff-coloured blur or cloud, just above the southern horizon, rapidly approaching then passing me, about on a level with my horse's head, to fade out of sight in a couple of minutes in the north ; soon to be succeeded by another and yet other flocks in endless succession, each appearing at the same point as the one before, following the same line, as if a line invisible to all eyes except their own had been traced across the green world for their guidance. It gave one the idea that all the birds of this species, thinly distributed over tens of thousands of square miles of country, had formed the habit of assembling, previous to migration, at one starting-point, from which they set out in successive flocks of a medium size, in a disciplined order, on that marvellous journey to their Arctic breeding grounds."

Although migration may at times follow a coast or a main river valley, and movement be restricted for the most part to these or other narrow paths, there are other times when migrants seem to advance on a wide front. The immigration of winter visitors and birds of passage from Scandinavia, for instance, impinges upon the eastern seaboard of Great Britain along the whole of its length from the Shetland Isles to the Humber. The route across the northern part of the North Sea, therefore, takes the form of a belt some hundreds of miles in width, although when once the immigrants reach our coast great numbers of them turn southwards along it and thus become concentrated on a relatively narrow path. According to Lynes the Mediterranean is also traversed by migrants mainly in

three broad belts—at the eastern and western ends and in the region of Sicily and Malta.

In the case of transcontinental migration there is no reason to believe that flight is always or even commonly restricted to particular narrow routes which follow river valleys and the like : Geyr von Schweppenburg (1924), for instance, states that migration across the Sahara is not confined to any narrow paths. Similarly, recent observations by Moreau show that, in spring at least, large numbers of migrants are to be found resting in the oases which lie in the Libyan Desert a hundred miles or more west of the Nile valley, although these places apparently lack practically all the common resident birds of Egypt. He has also seen numerous birds on actual passage across the desert, and he found no evidence that they all converged on the oases, although apart from these the desert presents an uninterrupted expanse of about twelve hundred miles, from south to north, of some of the most inhospitable country in the world. Moreau has also noted, in common with others, that migrants enter and leave Egypt in more or less equal numbers all along the north coast, and he believes that they traverse the country southwards or northwards, according to season, in complete indifference to the natural disadvantages of the lines on which they move. This conclusion is the more surprising because, *a priori*, Egypt would appear to present the conditions most favourable to migration along a narrow route. The Nile valley, running in the required direction, affords water, food, and shelter throughout the journey, while the country on either side, and particularly on the west, presents almost continuous desert conditions of the utmost severity : the desert traverse, moreover, immediately follows or precedes a long sea-crossing. Yet, although some birds follow the Nile, it seems that there may be no special concentration along its course, and that it is observers rather than birds that are restricted to the narrow route ! This does not, of course, necessarily mean more than that the Nile route is a very broad track, as there is no evidence that migration would be similarly observed in the desert for an indefinite distance westwards. Even so, it is difficult to see that the river can serve any purpose, as a guide or otherwise, to migrants which are apparently flying parallel to its course, but at a distance of a hundred miles or more.

Further to the south, in Darfur, Lynes has recently confirmed and extended the few records of earlier observers

which go to show that some migration takes place through even the most inhospitable desert regions. He concludes, however, that there is an important concentration along the course of the White Nile, and, second only to this, another concentration along the line of the Divide Range between Darfur and the Chad Territory, the migration through the intervening 500 miles or so of plain being relatively slight. He suggests that the Divide Range route may possibly represent the farther southward course of the migrants which cross the Mediterranean in the Sicily-Malta area, just as the Nile route is doubtless followed by those which cross the Levant.

Incidentally to the question of transcontinental routes, it may be said that even high mountain ranges are by no means insuperable barriers to migration.

Using the term in its widest sense, a migration route may, therefore, be anything from a narrow path adhering to some definite geographical feature such as a coast-line, to a broad tract leading in some general direction or at the most following the main trend of the land-masses. The extreme case is that in which the belt traversed by the migrants corresponds in width to the whole breeding range of the species.

It has been argued that a route begins to exist when there is some degree of concentration, however small, and when the migration area has thus less width than the breeding range from which the birds are drawn. That may be so, but it does not seem clear that a useful distinction can be drawn as between two different types of migration, one in which migration is concentrated into certain routes, and one in which the advance takes place, so to speak, along the whole available front. It is probable that every gradation exists between the highest degrees of concentration and of diffusion. It is also more than likely that in cases where the total migration belt has the extreme width, it may yet contain tracts of greater and less concentration.

It seems possible, accordingly, to say only that there is a common tendency for migration movements to become concentrated into more or less definite routes, and that in the highest degree of concentration these routes may be quite narrow paths closely following some appropriate geographical feature.

The subject, it will be seen, has now outgrown the dispute which arose among an earlier generation of ornithologists as to whether such things as routes existed. Palmen

expounded the doctrine of routes in exaggerated form, and his critics maintained that migration followed merely certain general directions without special concentration. Neither extreme view is wholly true : each has a measure of justification. The later tendency, in some quarters, has been to admit both views as separately true in different cases and so to distinguish between two kinds of migration. As has been said above, however, there may well be only one kind of migration, and while it may vary between one extreme aspect and another, there is probably every gradation between these, and possibly no reality in the suggested distinction.

Palmen and his followers extended their general theory into an attempt to define the principal European migration routes. In the absence of anything approaching adequate data they did so largely on hypothetical grounds, and often, as Herman showed, quite inconsistently with each other's views. Two main sources of error are now apparent. In the first place, the supposed routes were often made to follow geographical features which the particular author thought, on *a priori* grounds, would be followed by the birds. In the second place, too much stress was sometimes laid on the accident of observational opportunity which had caused certain places to become better known than others in respect of the movements there taking place. The island of Heligoland, for example, was so famous on account of Gätke's observations there that there was a tendency to exaggerate its objective importance. Gätke himself was no believer in exact routes, for which the only conditions he knew provided little evidence, and he maintained that Heligoland was no more than a good point from which to observe migration, which was elsewhere equally important but apt to pass unnoticed. The little island certainly lies in the path of important movements, but it is unlikely to be an important point in determining routes, lying as it does in a quite narrow stretch of sea over which movements take place on a relatively broad front.

At the present time one is able to draw upon a much greater body of exact evidence with regard to the principal directions of migration movements in Europe, but one must still be cautious in attempting to define routes. It must be remembered, too, that whatever main routes may be described, there remain a multitude of tributary and separate minor routes. It may, indeed, be said that the whole Continent is crossed by migrants in greater or smaller

numbers, often on intersecting lines. The main routes are, therefore, only those paths along which the tendency to concentration is especially noticeable.

Lucanus defines three main European routes, here taken in their autumnal directions. The first is the Western Coast Route, following the eastern and southern coasts of the Baltic Sea, the south coasts of the North Sea and English Channel, and the Atlantic coasts of France, Spain, and Portugal. Secondly, there is the Italo-Spanish Route, coming south-westwards from Russia to the head of the Adriatic Sea, then westwards through northern Italy and along the south coast of France, and southwards and south-westwards again along the eastern side of Spain : an offshoot turns southwards to Corsica and Sardinia. Thirdly, there is the Adriatic-Tunisian Route : this diverges from the second route at the head of the Adriatic, follows southwards one or other coast of that sea or some feature of Italy, and thence, direct or by way of Sicily, to the African coast in the region of Tunis. To migration south-eastwards towards and through the Balkan Peninsula he does not apparently allow the same major rank.

The directions of migration in the British area have already been considered (Chapter II). According to the view taken by Lucanus the migration, by way of Great Britain, from the north and the north-east would be tributary to his Western Coast Route, while the migration reaching the south of England from the east in autumn would be an offshoot from it.

In his studies of the migrations of Hungarian birds, Schenk (1922) also recognises the importance of the Italo-Spanish route, which he calls the *Via padana, ligurica, hispanica*. The equivalent of the Adriatic-Tunisian Route of Lucanus he subdivides into a *Via padana tyrrhenica*, and a *Via adriatica-occidentalis, siciliensis, tunesica-algerica*, the last also having a south-easterly offshoot in a *Via adriatica-orientalis, ionica*. It seems to be more than doubtful, however, whether existing evidence provides any sure basis for this theoretical elaboration, which one fears may be leading back to the errors of Palmen and his school. The attempt at an exact nomenclature, too, tends prematurely to crystallise ideas which overreach sound knowledge of the actual facts, and may possibly lead theorists into a maze of pedantry in further subdivisions and elaborations altogether lacking basis in reality.

Boubier has suggested that the migration routes of

Palæarctic species may be represented by fan-shaped tracts spreading towards the north and converging towards the south. Of these "fans" he defines five, as follows: (1) The European-Senegambian—converging from Greenland and Siberia, through Western Europe, to western Africa; (2) the Caucasian-Zambezian—converging from Eastern Europe and western Asia, through Egypt and the Red Sea region, to south-eastern Africa; (3) the Aral-Malabaric—converging from Eastern Europe and Central Asia, through Baluchistan, to western India; (4) the Himalayan-Indian—converging from the Himalayan region to the plains of India; and (5) the Siberian-Malayan—converging from eastern Siberia to eastern India and the Indo-Malayan peninsula.

Tracts of this kind may usefully represent the general directions of migration, and to that extent Boubier's theory can be brought into accord with the known facts, but the vexed question of concentration into special routes is avoided rather than solved. It seems doubtful, also, whether the fan-shape of the tracts expresses any important truth. A certain amount of convergence southwards must admittedly take place owing to the narrowing of the land-masses in that direction, but Boubier's map seems to exaggerate the tendency towards narrowness in the longitudinal range of species in their winter quarters: further information from such regions as Central Africa might well dispel this view, and in the case of his fifth tract he has apparently had to abandon the attempt to give it the typical fan-like form.

Passing reference may here be made to the question as to whether important migration routes traverse the Alps, about which ornithologists having special knowledge of the region are by no means agreed. Bretscher holds that, with the possible exception of Swallows, few birds cross the Alps to an important extent. This conclusion is based on a study of arrival dates in Switzerland, from which it is inferred that most of the birds penetrate that country from the south-west and west, and not over the main ranges. On the other hand, De Burg maintains that there is much migration across the Alps, a conclusion which he bases on personal observation at many of the passes and other high points as well as on a consideration of more general data. Alippi has made a careful geographical analysis of the Italian records of rare wanderers from different directions, but it cannot be said that this throws any direct light on the question of the routes by which that country is reached

by birds from the north. In view of the controversy on the point, Von Tschusi recently reviewed the evidence which exists in the shape of published records of transmontane flight, and he was led to the conclusion that much probably takes place that escapes observation.

According to Cooke the following main routes are followed by migrants between North and South America : (1) From Nova Scotia southwards across the Atlantic Ocean to the Lesser Antilles, reaching South America in the region of the Orinoco delta ; (2) From Florida south-eastwards by the Bahamas and Haiti to the Lesser Antilles and the same part of South America ; (3) From Florida in a less easterly direction by way of Cuba and Jamaica to western Venezuela ; (4) In a broad belt across the Gulf of Mexico from the south coast of the United States to Central America ; (5) Along the Mexican coast bordering the western side of the Gulf ; (6) From the central United States through Central America ; and (7) Along the Pacific coast. It might be argued that these routes taken together account for the whole width of land and crossable sea. The definition of the routes, however, depends on evidence that particular species are restricted to certain of them, and do not occur along the courses of others. Thus the Black-poll Warbler (*Dendroica striata*) appears to avoid Central America, and to reach the United States in spring by way of Cuba and Florida. The Cliff-Swallow (*Petrochelidon lunifrons*), on the other hand, comes north-westwards through Central America and then northwards through Mexico : the birds for the eastern United States must then turn north-eastwards, so that their complete path would be roughly a semicircle.

Farther north, much migration takes place along the two coast-lines of North America and also centrally along the great valley of the Mississippi. In the extreme north, that is in the region of the Mackenzie River, there seems to be a great convergence of routes : eastwards along the Arctic coast or through Alaska, north-eastwards from the Pacific coast, northwards overland, north-westwards overland by way of the chain of great lakes, and westwards from Hudson Bay.

It has been suggested that routes followed in spring differ from those followed by the autumn movements, tending to be more direct. Gätke held that in autumn the movements which he observed followed two sides of a triangle—westwards over Heligoland, but afterwards turning south—and

that, in spring, return was made direct by the third side in a north-easterly direction. His evidence was purely negative. Spring migration, as has been noted, is often more rapid than the corresponding autumn movement: there are fewer birds, and altogether the events are less conspicuous. (Eagle Clarke has noted, however, that the spring passage of Swallows and a few other species is the more conspicuous of the two movements at Fair Isle.) Coming in the opposite direction, and perhaps travelling by different stages, birds may also tend to pass given points at different times of day or night and to rest at different places. It may, therefore, be an accident of observation, and no more, that certain routes appear to be neglected in spring.

The positive evidence is now by no means negligible. It may be said that the experience of European observers is that most autumn movements have corresponding and opposite spring movements which follow equivalent directions, and that important alternative routes for spring movements have not been noted. (Some evidence obtained by Riviere, which indicates a possible exception to this general rule, has already been quoted in Chapter II.)

In North America there appear to be cases in which quite different routes are used in spring. Thus Cooke holds that in autumn the American Golden Plover (*Charadrius dominicus dominicus*) migrates from its breeding grounds on the Arctic tundras south-eastwards to Labrador, and then southwards by way of Nova Scotia and over a wide stretch of the Atlantic Ocean to the Lesser Antilles and South America; and that in spring it returns by way of Central America, across the Gulf of Mexico to the mouth of the Mississippi, and thence directly northwards through the centre of the United States and Canada to the breeding area. Similarly, he states that the Bobolink (*Dolichonyx oryzivorus*) leaves the United States by way of the Bahamas and Cuba and so across to Venezuela, but returns through Central America and across the Gulf of Mexico. Again, the breeding area of the Connecticut Warbler (*Oporornis agilis*) lies between Lake Michigan and Lake Winnipeg: in autumn the birds come eastwards to New England and travel southwards along the Atlantic coast to Florida and then across the sea: in spring they enter the country by way of Florida once more, but then avoid the Atlantic seaboard and travel directly north-eastward over country in which the species is not found during autumn passage. It is not easy, of

course, for European ornithologists to assess the value of the evidence upon which these conclusions, so strikingly different from their own experience, are based, and the statements must here be quoted without critical appraisement.

To what extent migration routes remain constant is an extremely difficult matter to decide. There is no doubt, certainly, that the general directions of the principal movements are always the same. There is also no doubt that at some places the movements are repeated year after year with great similarity in detail. This seems to be notably the case at the south-eastern corner of the Baltic, where the German Ornithological Society have a permanent observatory at Rossitten, and this place is of special interest because the movements are there restricted to a definite narrow path, as can be readily seen under the conditions for observation which prevail.

On the other hand, theoretical objection on meteorological ground has been taken, by Stubbs (quoted by Coward) and others, to the whole idea of constant routes. It is argued that once a bird is launched on migration flight its direction must be greatly affected by the movement of the whole body of air in which it moves and also by the rotating cyclonic currents within this. These factors, of course, vary from day to day and from hour to hour, so that even birds departing at short intervals from the same point and in the same initial direction would necessarily be borne on different, sometimes widely different, courses. The theory, however, seems to prove too much. Pushed to its logical conclusion it would negative the known constancy of the general directions of migration movements, about which there can nowadays be no room for doubt. To reconcile the two sets of facts it therefore seems necessary to assume that, except in the case of very strong winds, the migrants can adjust their flight to correct the effects of the external factors, or that if they are carried out of their course they regain it at the first opportunity. This leads to the question of the manner in which migrants are guided on their journeys, a problem reserved for further consideration at a later stage. It has, of course, to be admitted that birds flying without the aid of landmarks must, like aviators flying above a continuous stratum of clouds, be unable to gauge the effect of the changing directions and velocities of the air-currents within which they are moving.

From a consideration of this point it is not surprising to

find that although the main directions of migration movement are constant there is evidence of some variations in detail. From a long experience of migration as observed on the Isle of May, off the east coast of Scotland, Baxter and Rintoul have concluded that there are alternative routes which depend upon the meteorological conditions. They find that when easterly winds prevail in autumn, migrants from Northern Europe are most abundant, and various Asiatic species, never found under other conditions, are commonly recorded. The conclusion is that when these winds blow many migrants leaving, say, Scandinavia are borne, or induced to fly, towards the British Isles, whereas they would otherwise travel southwards by a route lying farther to the east. Weigold has more recently recorded a similar opinion as to the existence of alternative routes depending upon meteorological conditions, and his experience on Heligoland is in an interesting way complementary to that of the observers just quoted.

Further evidence on the point would be of much interest. One would like to know the extent of the variations which occur, and whether one alternative can be regarded as the normal, and others merely as abnormal deviations from it which possibly involve failure to find the usual winter quarters or which even lead to destruction. Let it be remarked, however, that in all evidence on the subject it is very necessary to consider the possible effects of different conditions upon the opportunities for observation, as distinct from any effects upon the events which actually take place.

The question of the stability of routes arises also in relation to expansions of breeding range. Thus the Shore-Lark (*Eremophila alpestris flava*) has spread westward into arctic Norway within recent times, and according to Gätke a new migration route came into being about 1847, and the species then became a common bird of passage, at both seasons, on Heligoland. Still more recently, namely, in 1879, the Shore-Lark became a regular visitor to the east coast of England : Pashley stated, with regard to the Norfolk coast, that in the 'sixties he used to give five or ten shillings for a specimen, but that in the late 'nineties he had them brought in by dozens. On the other hand, Cooke states that when the Bobolink (*Dolichonyx oryzivorus*) extended its breeding range westwards in North America it adhered to the old routes, although a thousand miles were thus added to the journey. Other examples might be quoted. Precise

information as to the behaviour of birds introduced into new and distant areas by human agency would be of interest.

Little can be said about the flight-lines of individual birds, as distinct from the observed directions of general movements. The flight of any migrant obviously traces a mathematical line, whether it be straight, curved, or crooked. The point at issue is the extent to which this line is necessarily defined, and, so to speak, predetermined: does it follow some definite path? If so, in relation to what geographical or other factors is that path determined? The problem of orientation will be discussed at a later stage, and here the question is one of fact: the evidence, unfortunately, is wholly circumstantial.

One possible view is that the flight-line of every migrant follows some given path, defined in some way by a series of landmarks. In certain places very many of these paths become concentrated in a common course, thus producing what has been described already as the route of a general movement. In other places, where the migrants appear to advance, not in column on a narrow front, but in widely extended formation, the flight-lines of the individual components of the army are still to be thought of as following particular paths. It is thus conceived that where a migration route takes the form of a wide belt this is made up of a large number of separate and clearly defined paths running parallel to each other.

The opposite view is that flight-lines are not defined except as regards their general direction, and that the details of the course followed are consequently largely fortuitous.

An objection to the first view is that it is difficult to conceive how the component paths, in the case of migration on a wide front, could be defined when they do not follow any very obvious geographical features. An objection to the second is that it is difficult to account for the existence of routes of general movement except on the assumption that the component paths are defined in some common way. It may be asked whether the concentration of flight-lines at certain places cannot be explained in some other way, and with regard to some instances an affirmative answer seems possible. In places the shape of the land-masses would naturally tend to produce some concentration, as would the occurrence of desert or perhaps mountainous regions in others. Again, in the case of sea-fowl and shore birds coasts would naturally be followed if they trended in the

right general direction : so also might river valleys or chains of lakes be followed by any birds to which these offered the kind of resting and feeding places which are preferred. But no suppositions of this kind can explain away the tendency to follow coast-lines, even where easy and perhaps shorter alternative routes are possible, which is shown by many birds for which neither sea nor shore nor inland water ordinarily has special significance.

It cannot be denied, moreover, that where migration is confined to a definite narrow route this is sometimes followed with a detailed exactness which shows that the geographical feature concerned is indeed important as a guide. The writer has already described his experience of the migration of the Hooded Crow (*Corvus cornix*) as observed on the coast at the south-eastern angle of the Baltic Sea (Chapter III). There the stream of migrants was of no width, and there were no parallel streams within sight. The birds followed the line of the shore with some accuracy, and where this line bent inwards away from their course they found themselves flying out to sea : after a very short distance the deviation was corrected and the flocks wheeled in adjustment to the new direction of the coast.

These difficulties have naturally produced a tendency towards a compromise which utilises both the extreme theories, and this has been variously formulated by different writers. This brings one back to the idea, already mentioned, that there are two kinds of migration—one in which certain relatively narrow routes are followed, and one in which movement takes place on a wide front. It is supposed, for instance, that in the case of the former the flight-lines are defined in relation to conspicuous geographical features and so naturally have a common path, and that in the case of the latter only the general directions of the flight-lines are determined and so a more diffuse movement results. It has to be assumed, moreover, that the same birds may be capable of both kinds of migration at different times or places : a mere general direction would be followed in a wide-front movement across sea or plain, and then definite landmarks would be picked up and concentration would take place in the definite route of some coast-line or river valley. This hypothesis may perhaps fit the facts as they are at present known ; but, remembering the scientific maxim that a complex explanation should not be adopted where a simpler one will serve the purpose, one is reluctant to accept it as more than a tentative suggestion.

Certainly it introduces new difficulties into the already complex theoretical problems which migration presents to the biologist (Chapter XX). Meanwhile, more facts are needed.

Before concluding this discussion of migration routes and flight-lines, mention may be made of the idea that the directions followed by migrants at the present day correspond to the paths of dispersal along which the species originally spread in its gradual extension of range from the hypothetical cradle of the race. With this may be coupled the once popular theory that the routes followed by migrants when crossing the sea correspond to the sites of land-bridges which existed there in former geological epochs. That there is such correspondence in some places is true enough, but there is no possible means of proving any relationship: disproof, on the other hand, can rest on no better ground than the negative evidence provided by the lack of any similar correspondence at other places.

Schenk (1924) has been particularly critical of the idea that migration routes may be relics of the paths of great distribution movements in the history of the species concerned. He points out that the routes known to be followed to-day correspond to the geographical features of the present age and not to those of some earlier geological period : it is the coasts of present-day Europe that are followed and not those of lost continents of the dim past. The objection, however, does not seem to be entirely valid. The geological changes have taken place with extreme slowness, and it does not seem extravagant to suppose that the evolution of migration could keep pace with it, and that modifications in conditions would lead to modifications in performance. (Mention has already been made of evidence as to the effects of extensions of range of recent date.) It does not, therefore, follow that migration paths have no history, because they have changed with the times : the biological factor is dynamic, not static. It does not even follow that some oversea routes of to-day had not their origin in routes determined by land features long since submerged. Yet it may safely be said that too much has frequently been made of what may be termed the historical theory of the nature of migration routes, and that the available evidence is at once neutral in regard to it, and positively in favour of the view that many routes of to-day correspond to geographical features of the present time.

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CHAPTER VI

THE RELATION OF WEATHER CONDITIONS TO BIRD-MIGRATION

"And there went forth a wind from the Lord, and brought quails from the sea, and let them fall about the camp, as it were a day's journey on this side, and as it were a day's journey on the other side, round about the camp, and as it were two cubits high upon the face of the earth."

NUMBERS, xi. 31.

Obvious general relationship between migration and seasonal climatic changes—Question as to relationship between variations in migration and immediate weather conditions—Conclusions of Eagle Clarke on British data—Certain conditions at point of origin of a movement predispose to migration therefrom—High pressure at starting-point favourable both in autumn and spring—Direction of wind has no important influence—Falling temperature at starting-point also favourable in autumn, and rising temperature in spring—Unfavourable conditions may be encountered *en route*—Storms and fog—Invalidity of observations at a single station—Similar conclusions of Defant as to pressure—His belief in importance of favourable winds—Similar conclusions of Hegyfoky as to pressure and temperature—Schenk on the migration of Woodcock—Similar conclusions of Cooke in North America—Contrary view of Bretscher—Conclusion.

FROM the nature of the case there is obviously a general relationship between the events of bird-migration and the sequence of meteorological changes which constitutes the annual cycle of the seasons. Migration is adapted to climatic conditions and to the seasonal changes therein.

This broad fact is evident not only from the general seasonal character of migration, but also from the differences which exist in the average dates of corresponding movements at places which are subject to different climatic conditions. The geographical incidence of migration events is related to the geographical incidence of seasonal climatic changes. Thus, the arrival of a summer visitant species may be more than three months earlier in the south of Europe than in the north, corresponding roughly to the delay in the return of spring.

It may be noted in this regard that although for a given region there is an optimum mean temperature related to the date of immigration of any species, the figure is not necessarily identical for different regions. The general tendency is for arrival to take place at lower temperatures

in higher latitudes: in other words the immigration may advance rather more rapidly than the isotherms. Incidentally it may be remarked that the movements of species arriving late in the season are completed within a shorter period than those of species which are earlier migrants.

The differences which are observable in the dates of arrival in different regions do not depend merely on latitude, but are shown also between places in the same latitude which have different climates. In a restricted region, even, differences may be noted between places no great distance apart but differing in altitude. Cooke (1904), for instance, records that there is an average difference of three and a half days between the arrival of corresponding summer visitors at two localities in North Carolina, which are just over 200 miles apart and in practically the same latitude, the later place being 1700 feet higher and having a mean temperature which is less by 5° F. Some further evidence on these points will be detailed in a subsequent chapter dealing with the Swallow.

Although this general relationship between migration and *climate* is obvious, the existence of a relationship between migration and *weather* has been the subject of much controversy. It is, of course, not necessarily the case that, because migration is a seasonal phenomenon, there is a close correspondence between the individual events and the day-to-day meteorological changes.

The question really takes this form: Migration is related to the seasonal cycle of climatic changes, but are the differences between migration in one year and another related to corresponding differences in weather? The cycle of the seasons and the sequence of bird movements are both annually recurrent phenomena which are constant in their general aspects, but they both show variations from year to year: are these variations related, or are the differences in migration, as between one year and another, purely fortuitous?

Roughly speaking, one may say that the extreme range of year-to-year variation in the dates of spring immigration in temperate latitudes is about a month—that is, the difference between an exceptionally early date and an exceptionally late date for a specified event: but the average amount by which one year differs in this respect from the mean of all years is a matter of only a few days. To take a concrete case from the reports of the Migration Committee of the British Ornithologists' Club, the Swift (*Apus apus*)

was first recorded in England, in the years 1905–13, on 12th, 21st, 23rd, 27th, 19th, 23rd, 25th, 17th, and 14th April. The average of these dates is 20th April, the greatest variations −8 and +7 days, and the mean deviation from the average 4 days. The Swift is cited because the dates of first appearance are a more reliable index of its movements than is the case with many species, in which the first principal arrivals are apt to be masked by the more or less erratic appearance of advance stragglers.

An interesting attempt at a statistical proof of the existence of a relationship between variations in migration and variations in meteorological conditions has recently been made by De Lury. He took as his data the records of the first arrival of certain summer visitors in France kept for eighty-six years by members of the Chandon family at Montdidier. These figures he analysed with a view to finding whether there was any correspondence with the meteorological cycles which are known to be related to the 11·5 year sunspot periods (*cf.* Introduction). By superimposing and averaging seven of these periods he found that the Cuckoo was first heard, on an average, nine days earlier in the years of sunspot minima than in the years of sunspot maxima, intervening years showing appropriate intermediate values. For the arrival of the Swallow a similar but much slighter correspondence was found. This result suggests in a general way that the variations in the dates of migration are not fortuitous, but are related to variations in meteorological conditions.

The direct study of the relationship between migration and weather is beset with many difficulties, and is not one which can well be undertaken by the individual observer. The subject can be approached with success only when knowledge is available of the meteorological and ornithological facts for the whole region affected by any particular movement. This condition is not easily satisfied, but in the British area it has been fulfilled in the mass of data collected by the Migration Committee of the British Association for the Advancement of Science and so ably analysed by Eagle Clarke. A summary of the conclusions reached in that inquiry will afford a good foundation for further consideration of the subject.

There are, of course, two possible ways in which weather conditions may influence migration : the conditions at the starting-point may predispose to the inception of movements, and the conditions *en route* may affect the progress

of movements already begun. The one influence may be of fundamental importance in relation to the times and magnitudes of the principal movements, while the other is to be regarded rather as an accidental circumstance.

Eagle Clarke concludes that the weather conditions prevailing in the area of origin of a movement have an important influence, while the weather conditions prevailing at the destination do not affect the question as to whether the flight is to be undertaken or not. Given favourable conditions at the starting-point at the proper season, a movement will take place therefrom whether or not favourable conditions prevail in the area in which the later part of the journey must lie. This conclusion is, indeed, not different from what one would expect to find if weather conditions have any direct influence at all, but it is fortunate that it has been so well established on such a wide basis of observational data.

In north-western Europe at least, the general weather conditions which are favourable for emigration from a given region are anticyclonic pressure conditions, with settled fine weather and light winds. The existence of a cyclonic depression, on the other hand, with bad or unsettled weather and high winds, is against the occurrence of movement from the region affected. Thus, for example, the type of weather most favourable for migration across the North Sea, whether in autumn or in spring, is that in which a large anticyclonic area lies to the east of Great Britain and the wind is mainly from the south-east. At the same time this type of weather distribution is unfavourable for migration between the British Isles and Iceland, a low pressure area lying to the west of our shores.

In the case of migration between Scandinavia and Great Britain both countries frequently lie within the same area of favourable or unfavourable conditions, and it is then immaterial in which direction, according to the time of year, the movement is to proceed. Thus it happens that the same general conditions may be favourable both in spring and in autumn. Where only one of the countries falls within the favourable area the direction of migration according to the time of year is all important. Favourable conditions over Scandinavia with unfavourable conditions over the British Isles will be associated with migration from the former country in autumn, but not with migration from the latter country in spring. Where the respective conditions at the points of departure and of arrival are

different it is those at the point of departure which are material.

It is considered by Eagle Clarke to be clearly established that emigration tends to take place from a given area when there occur in that area at the proper season the conditions which have been defined above as favourable. Similarly, emigration from a given area is delayed by unfavourable conditions there. The greatest emigratory movements are those which occur when favourable conditions supervene after a period of adverse conditions during which migration has been held up.

Wind, according to the same authority, is a relatively unimportant factor, contrary to popular belief. High winds are unsuitable, and are in any case generally associated with the pressure conditions already described as unfavourable. Given a light or moderate wind, however, its direction appears to be immaterial. During the type of weather already described as favourable for migration across the North Sea—the direction of which is south-westerly in autumn and north-easterly in spring—the prevailing wind is from the south-east and thus at right angles to the line of flight. During the opposite conditions, which are those most unfavourable for migration along the same route, the prevailing winds are from the north-west, which would also be at right angles to the line of flight. Examples might be multiplied, but all would lead to the same conclusion that the direction of the wind is an unimportant factor, and that when migrants travel with the wind it is a coincidence—the migration and the wind are not directly related, but are respectively influenced and caused by the pressure conditions at the point of origin.

In addition to pressure conditions, temperature exerts an important influence. A falling temperature in autumn and a rising temperature in spring are the conditions predisposing to migration, and here again it is the temperature at the place of origin and not at the destination which matters. A rise of temperature in south-western Europe in spring will cause a movement of summer visitors towards our shores even if wintry conditions still prevail in the British Isles. Similarly, a rising temperature in the British Isles predisposes to spring migration to Northern Europe, and a falling temperature in the British Isles predisposes to autumn emigration to the south.

Not unnaturally, the most favourable circumstances of all are those in which pressure and temperature conditions

are both good and thus act together. During a long period when pressure conditions remain constantly favourable the effects of rising or falling temperature, according to season, will be marked by fluctuations in the magnitude of the movements taking place. Again, favourable temperature conditions may by themselves suffice as predisposing factors if the pressure conditions are no more than mildly adverse.

Eagle Clarke's general conclusion is, then, that the weather conditions at the place of origin of a movement predispose to the occurrence of migration, but that the migrants are naturally affected during their flight by such other conditions as they may encounter. If the favourable conditions at the point of origin extend over the whole distance to be travelled at the particular stage, so much the better. If unfavourable conditions are encountered *en route* there may be a cessation of movement at that point, a banking up of the migratory stream; or if this happens at sea there may be serious loss of life, as has frequently been recorded, before the journey is accomplished.

The conditions most dangerous and unsuitable for flight are, on the one hand, stormy weather, with high winds and heavy rain, and, on the other hand, fog. Storms are liable to be encountered, as has been seen, when the favourable conditions predisposing to migration are restricted to the area where the movement originated, and do not happen to extend over the whole extent of the journey: the same effect might be produced by a sudden change in the meteorological situation as a whole. Fog at sea, however, is not uncommonly associated with the type of weather which is otherwise most favourable. It is a serious obstacle to successful flight and appears to result in loss of direction by many of the migrants. It is also during fog, and thick weather generally, that migrants are most frequently lured to destruction at the lanterns of lighthouses and lightships, a point to which reference has already been made in a previous chapter.

The foregoing conclusions will give force to the statement already made that the subject is not one which lends itself to study by the individual observer. The arrival of birds is much more readily noted than their departure, but the weather conditions at the point of arrival are not those to which importance is to be attached. In observing the autumn migration of shore birds on the Dutch coast, Bonhote found that a low barometric pressure was associated with

the chief periods of influx: he would not have wished to give undue weight to evidence collected over only a short period, but the observation may be taken as illustrating the point in question. Quite possibly the low pressure here was merely a natural concomitant of high pressure in the distant area of origin and was of no direct importance. Alternatively, the low pressure may have constituted an unfavourable local condition which led to a banking up of the migration stream and a congestion of birds, rather than a condition favourable to increased movement.

It may be added here that in all studies of the relationship between weather and migration it is necessary to keep in view a possible source of error, namely, the influence of weather on observation: under certain conditions migration may be more readily observed without there being, in fact, any increase in the volume of migration, and the records will thus be swollen for a quite secondary reason. In other words, it must be remembered that the observational data refer not to the whole of migration, but only to observable migration. This factor must be discounted as occasion demands, in accordance with the nature of the data obtained and the extent to which they may be affected in this way.

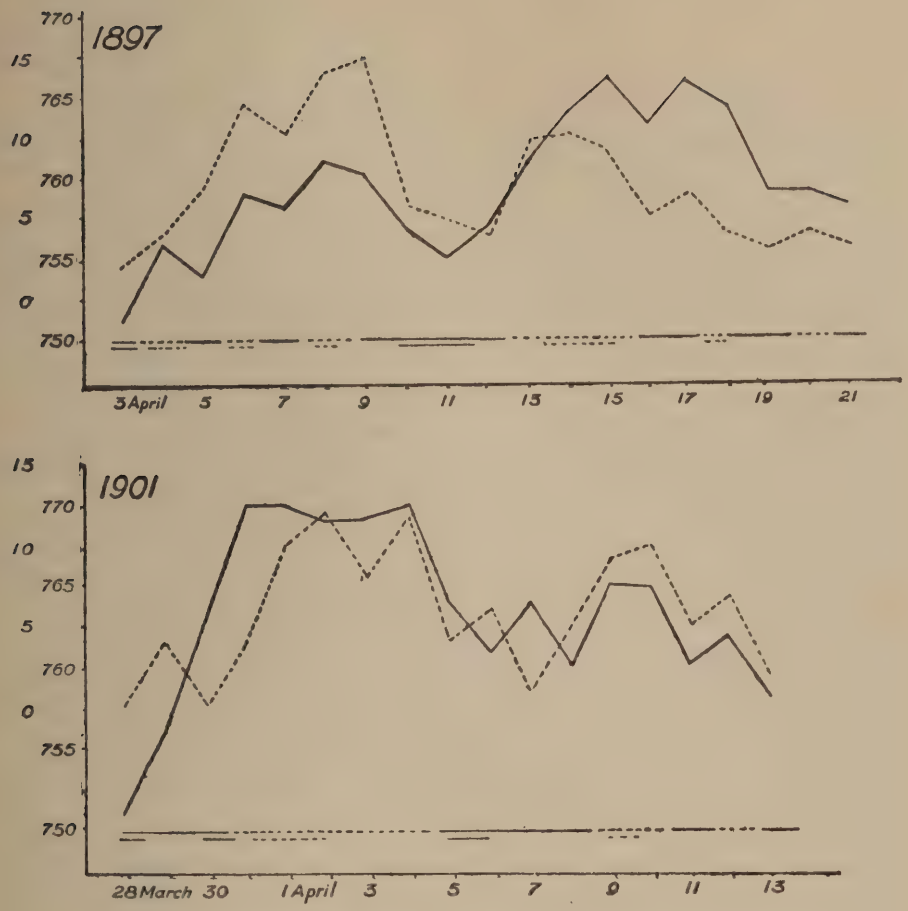
With the foregoing conclusions based upon Eagle Clarke's work in the British area, it is interesting to compare those reached by Defant, a meteorologist who investigated the ornithological data for the spring migration in Austria collected for seven consecutive years by Lorenz and Sassi. His paper is an important contribution to the subject, and the evidence is published very fully, with tables and analytical diagrams: the methods used can thus be checked in detail, and seem to be notably free from liability to subjective errors. Four species are dealt with, namely, the Starling (*Sturnus vulgaris*), the Skylark (*Alauda arvensis*), the Swallow (*Hirundo rustica*), and the Cuckoo (*Cuculus canorus*). The arrival records for these, as presented by the ornithologists, have been mathematically examined in relation to the weather conditions in the Balkan region and in the western Mediterranean. In each case a close correlation was found between immigration into Austria and high barometric pressure over the Balkan peninsula. Further investigation showed also a good correlation between this immigration and the existence of a pressure gradient falling from east to west in the Mediterranean region, a situation in which the migrants would travel with a south-easterly wind behind them. It will be noted that this investigation,

so far as it goes, is in accord with the British experience as regards the importance of fine weather, indicated by high pressure, in the region from which the birds come. Defant, however, differs from Eagle Clarke in attaching direct importance also to favourable winds.

Hegyfoky, also a meteorologist, has similarly investigated the records collected by the Royal Hungarian Institute of Ornithology under the direction of Herman. His results have been published in a series of papers, but his general conclusion may be summarised in a few words. He finds that the immigration of summer visitors into Hungary is favoured by high barometric pressure and rising temperature in the region passed through, these conditions being commonly present when there is a depression over north-western Europe : the opposite conditions are unfavourable. In his opinion temperature is the more important factor.

Among the species dealt with by Hegyfoky has been the Woodcock (*Scolopax rusticola*), and his results in this instance have recently been summarised by Schenk with a description of the method employed. Eight years were dealt with and about 700 records of arrival were available for each. The year was divided into five-day periods or " pentads," and the percentage of the total of the season's records occurring in each period was noted. It was found that each year showed a " culmination " in a particular pentad, amounting to from 15·8 to 28·7 per cent of the total records for the whole season. In three of the eight years the culmination fell in the second pentad of March ; in one year it was a period earlier, and in the others it was respectively one, two, three, and five periods later. In each of the eight years the " culmination " occurred when the feature of the weather situation was an area of low atmospheric pressure to the north-west, *i.e.* in the region of the British Isles, with higher pressure in the area of observation. Schenk adds that " the first north-westerly depression which occurs at the end of February or the beginning of March brings the Woodcock to the coast of the Adriatic and the plain of the Drave." With the disappearance of this weather situation the main migration comes to a standstill, to be renewed—provided it was not previously completed—when the situation is next re-established.

Autumn migration of Woodcock in northern Germany, according to Schenk's summary (1924) of the observations of various authors, is favoured by a weather situation marked by a north-easterly depression, *i.e.* over northern



RELATION BETWEEN WEATHER AND THE MIGRATION OF THE SWALLOW.

After Defant.

Showing the correspondence between high barometric pressure to the southward and the spring immigration of the Swallow (*Hirundo rustica*) into Austria in two different years.

The thick curve shows the daily numbers of records of the arrival of Swallows in Austria (figures in outer vertical column).

The interrupted curve shows the daily mean barometric pressure for the Balkan and Adriatic region whence the birds are presumed to come (figures in inner vertical column, expressed in millimetres of mercury).

The horizontal line indicates the relation of pressure in the Balkan and Adriatic region to that of the region immediately to the west (centred on Sardinia): thick line, gradient rising from east to west; interrupted line, gradient falling from east to west.

Scandinavia, and Pittet is quoted as having reached analogous conclusions as regards Switzerland.

In North America much evidence has been collected over a long period of years by the U.S. Bureau of Biological Survey, aided by observers throughout the United States and Canada, and the data are especially valuable because they refer to so wide a region. From an analysis of more than 400,000 records Cooke (1911) drew conclusions which are in the main similar to those of Eagle Clarke, and which may here be conveniently quoted in his own words. " Local weather conditions on the day of arrival at any given locality are minor factors in determining the appearance of a species at that place and time. The major factors in the problem are the weather conditions far to the southward, where the night's flight began, and the relation which that place and time bear to the average position of the bird under normal weather conditions. Many, if not most, instances of arrivals of birds under adverse conditions are probably explainable by the supposition that the flight was begun under favourable auspices and that late in the night the weather changed. Spring migration usually occurs with a rising temperature, and the movements of autumn with a falling temperature. In each case the change seems to be a more potent factor than the absolute degree of cold. The direction and force of the wind—except as they are occasionally intimately connected with sudden and extreme variations in temperature—seem to have only a slight influence on migration." Cooke makes the reservation, on theoretical grounds, that the departure of birds from tropical winter quarters is unlikely to be influenced by weather conditions, and that the effect of these is, therefore, a secondary one operating during the later stages of the northward journey which come under observation. He also stresses the fact that the chief relationship is not with variations in weather, but with " average weather," that is to say climate, a point already dealt with at the beginning of this chapter.

It will be seen that all the writers so far mentioned are agreed as to the existence of a relationship between weather and migration, as shown in the variations in the latter from year to year, and that there is also a large measure of general agreement as to the factors which are important and as to the nature of the effects which they produce. The evidence refers to such different regions as the British area, Central Europe, and North America. The data have also been collected in different ways, for while the investigators on

the Continent of Europe and in America have had to rely largely upon observations of arrivals in inland districts, the British records in question were mainly of movement actually observed at light stations round the coasts.

Nevertheless, the existence of any relationship between weather and migration is denied by some. Bretscher, in particular, has taken a view which is diametrically opposed to that of the other writers. He bases his opinions upon the results of a number of elaborate and laborious statistical investigations which he has made. He has principally used collected observational records for many years relating to the relatively low-lying central region of Switzerland, and mainly to the arrival of summer visitors, but he has also examined similar data from Alsace-Lorraine. He takes the number of records of immigration and compares their daily incidence with the incidence of various meteorological factors taken separately, and he finds no correlation between the amount of immigration and the value of any particular factor in the weather.

He has paid particular attention to the question of temperature. The only relation which he finds is between the average date of arrival of a species over many years, and the average incidence of a certain mean temperature : this is no more than to say that bird-migration and progressive rise in temperature are regular seasonal phenomena, the variations in both sets of factors in different years being eliminated by the method. In other investigations he has compared immigration with the absolute temperature on corresponding days, and also with the relative temperature as measured by its being greater than, equal to, or less than the temperature on the preceding day. Similarly, he has dealt with wind direction, with absolute barometric pressure, and with the general barometric situation as indicated by the direction in which the principal depression lay. All these meteorological factors he finds, by his method, to be indifferent as regards migration.

The methods employed by Bretscher seem to be open to very serious criticism. For one thing, nearly all his meteorological data refer solely to the point of arrival and are therefore, according to the more general view, almost wholly irrelevant. For another, he lays special stress on his negative results in respect of such factors as absolute temperature, which his opponents have in any case not claimed as effective. In general, his methods do not appear to be truly analytical : no allowance, for example, is made

for a possible " lag " in the effect of meteorological factors, which should perhaps be taken for the day before, or some days before, the ornithological records. On technical statistical grounds, too, the methods used have been strongly criticised by Tollenaar, who says of one investigation that Bretscher had used no method which would have revealed a relationship if one existed, and that the negative conclusions are therefore valueless.

Lucanus, in reviewing the position, rather surprisingly comes to the conclusion that Bretscher's view is to be supported as against that of the other writers: the evidence with which he deals includes that of Defant, of Hegyfoky, and of some smaller German investigations not separately mentioned in this chapter, but no reference is made in this connection to the very important work of Eagle Clarke and of Cooke.

To the present writer it seems much more reasonable to consider that the negative conclusions reached by Bretscher cannot be accepted in face of the contrary evidence of a positive nature which exists in such large amount. Where a positive result has been obtained and repeatedly confirmed, and in the absence of convincing criticisms of the methods of investigation and deduction, the mere obtaining of a negative result cannot be taken as invalidating the conclusions. In these circumstances a negative result is more likely to be due either to some difference in the particular data examined or to a less suitable method of investigation. That Bretscher's methods are indeed open to serious criticism has already been shown: in the main, too, his conclusions are not exact opposites to those of the other writers here quoted.

It should be remarked that this chapter has dealt with spring migration and with ordinary autumn migration, to the exclusion of the late " weather movements " to which reference is made elsewhere. These movements are irregular, varying from year to year both in date and in magnitude according to the nature of the season. As they appear to be the direct result of severe weather, their relation to meteorological factors may be a different one from that of ordinary autumn migration, although if falling temperature at the point of origin may be taken as the instigating factor in these movements they are to that extent consistent with the usual principles. In temperate latitudes these movements do not take place until winter, when the regular autumn migration is practically completed, but it is not

impossible that in very high latitudes, where severe weather begins early, they may overlap and complicate the usual departure movements of the summer visitors there. Thus, in dealing with migration at the mouth of the Yenesei, in arctic Siberia, Haviland says that there seemed to be two groups of birds—" those whose return migration appeared to take place at the heyday of the summer, quite independently of weather conditions or food supply; and those whose southward movement was put off until the winter storms drove them away." The Grey Phalaropes (*Phalaropus fulicarius*), for instance, were all gone by 5th August, although the species is a late breeder, and several other birds had left while summer weather still remained and food was plentiful: for species in the second group the onset of the first wintry storm at the end of the month seemed to be the signal for departure.

Finally, it may be remarked that this chapter has been concerned with practical rather than with theoretical questions, and has accordingly dealt only with the observable correlation between the meteorological and the ornithological data. Consideration of the possible existence of causal relationships, which must not be hastily assumed, is postponed to the concluding part of the book. It may be well, however, to anticipate one point of some importance, namely that migration accompanies favourable weather conditions only when these conditions occur near the appropriate dates: the conditions occur at other seasons, *e.g.* midsummer, without any movement taking place. It is at least obvious, therefore, that the whole explanation of migration phenomena is not to be sought in the possible influence of weather.

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SOURCE OF DATA SHOWN ON DIAGRAM.—The diagram showing the relation between weather and the migration of the Swallow has been merely redrawn from one of a number of similar figures published by Defant (1913).

CHAPTER VII

IRREGULAR MIGRATION PHENOMENA

"And fainter onward, like wild birds that change
Their season in the night, and wail their way
From cloud to cloud, down the long wind the dream
Shrill'd; but in going mingled with dim cries
Far in the moonlit haze among the hills."

TENNYSON, "The Passing of Arthur."

Distinction between typical migration and less regular phenomena—Erratic wanderings—"Weather movements"—Occasional "irruptions"—Irruptions of Pallas's Sandgrouse—of the Rose-coloured Starling—of the Crossbill—of the Waxwing—of other birds.

TYPICAL migration consists of definite movements which are regularly repeated year by year, and it is to this that the term is restricted for most purposes in discussion of the subject. It is desirable, however, that some account should be taken, if only for purposes of comparison, of those other movements which are less regular in nature but which have nevertheless some of the characteristics of true migration.

There are, for instance, the annual but rather indefinite movements performed by some birds in the intervals between breeding seasons. These may be no more than erratic wanderings in search of food, such as those of some sea birds, and they may or may not have some definite directional trend. Perhaps it would be impossible to draw any sharp distinction between these movements and typical migration, for every gradation would probably be found between the most erratic wanderings and the most definite movements which follow the same course year after year. All these movements, too, have this much regularity, that they are punctuated each spring by a return to the breeding stations at the appropriate time.

Then, again, there are the late "weather movements" which occur in severe winters. These represent extensions and amplifications of the ordinary autumnal movements, except that they do not, of course, involve any of those species which in any case withdraw completely from high latitudes on the approach of winter. Among those species

which are not wholly migratory, or which migrate for only short distances, the number of migratory individuals may be increased or the journeys be extended in length by these weather movements. Severe weather occurring in spring may also produce a temporary retreat of recently arrived birds from their breeding localities, but there does not seem to be evidence that these reverse movements are more than local in their extent. In principle these movements differ from typical migratory movements in that they are performed under the compulsion of external conditions and not in advance of the real necessity, and that they are not regular but depend each year on the nature of the winter and on the severity, time and geographical incidence of the hard weather. The irregular phenomena may be regarded as superadded to ordinary migration rather than as distinct therefrom.

There are, however, certain movements which are irregular in an altogether higher degree. These are movements which occur only at long intervals and which in the most notable cases cannot be described as merely amplifications of normal migration. When they do occur, however, they may be quite definite in their nature and may closely resemble ordinary migrations except for the fact that they do not take place every year.

Pallas's Sandgrouse

By far the most remarkable example of an exceptional movement of this kind is that provided by the occasional "irruptions" of Pallas's Sandgrouse (*Syrrhaptes paradoxus*). The normal habitat of this species is in the desert region of Central Asia from Mongolia westwards to Turkestan, and in the extreme south-eastern portions of European Russia. Under ordinary circumstances it is not a great migrant: in parts of its range it is almost stationary, and although in severe winters it reaches the plains of China, it does not penetrate to India or to the eastern Mediterranean countries. At intervals of several years, however, an irruption takes place in spring in a north-westerly direction, and numbers are then recorded in Europe and as far as the British Isles. On these occasions the species may even breed, or at least attempt to breed, in the new countries which it reaches. There does not seem to be any very definite return movement: most of the birds probably perish, but survivors have been noted in the following year.

The first recorded "irruption" reaching the British Isles

was that of 1859, and specimens obtained in that year constitute the earliest evidence of the occurrence of the species in this country. This was followed in 1863 by an invasion on a great scale. Following a first appearance on 21st May the species became abundant in the British Isles during the summer and reached even the northern Scottish isles and the north-west of Ireland. Survivors were recorded in 1864. Small irruptions followed in 1872 and in 1876, and in 1888 the greatest known invasion took place. Early in March in the last-named year it was reported from eastern Russia that the Sandgrouse were on the move, and thereafter the birds spread all over Europe and reached the British Isles in May. Most of the British records were from the east coast, but again the birds spread to outlying parts of the country: it was estimated that from 1500 to 2000 birds reached Scotland. Many of the birds bred. Some survived until 1889, and in that year a nestling was found in Moray. Occasional birds were recorded in the British Isles in 1890, 1891, 1899, 1904, 1906 and 1907. In 1908 a considerable invasion was noticed over a large part of Europe, and there were records from several English counties. For 1909 there is a single record from Yorkshire.

In his summary of the 1908 invasion of Europe, Von Tschusi concludes that the main movement followed two lines. One lay to the north of the Carpathians and extended to the North Sea and across it to the British Isles. The other led by way of Roumania as far as southern Italy. A large flock noted in Roumania in November formed the subject of practically the only record indicating a definite return movement.

These movements are possibly to be regarded as sudden attempts at extension of range due to some imperfectly known cause. In support of this partial explanation there is the evidence of the successful establishment of a new colony in south-eastern Russia, where the species was apparently not previously a regular inhabitant, after the invasion of 1876. According to Remann, moreover, a more gradual extension of the breeding range into European Russia has taken place during recent years. The irruptions into Western Europe may perhaps, therefore, be considered to be exaggerated and extended phases of these more explicable movements.

With regard to the periodicity of the invasions, Elton suggests that the sunspot cycle of 11·2 years is in evidence, and that the larger invasions occur in every alternate

period, *i.e.* every 22·5 years. The figures do indeed seem to support this view, although it is necessary to assume that certain of the small invasions are of a subsidiary nature and should be grouped with the larger invasions near which they come rather than be taken as representing separate periods. The following table contrasts the theoretical periodicity with the actually recorded facts (for the British Isles), the dates of the major invasions being in both cases shown in heavy type:—

Theory	**1863**	1874	**1885**	1897	**1908**	1919	**1930**
Fact	1859	1872	**1888**	1899	1904	nil	?
	1863	1876	1889		1906		
	1864		1890		1907		
			1891		**1908**		
					1909		

It must be noted that the grouping of the actual dates shown above is no arbitrary one adopted to fit the theoretical requirements, but represents a natural division according to the occurrence of intervals of five years or more. It is to be seen that the major invasions do tend to show a periodicity of the order of 22·5 years, and that the minor invasions tend to occur either near the dates of the major invasions or else about midway between. (The birds recorded in 1864 and 1889 may all have been survivors from the previous years. The 1907 and 1909 dates refer to a single record only in each case. There are occasional records from the Continent for other years than those shown in the table, but none indicating additional irruptions of any importance.)

No small invasion about 1919 was noted, however, and it will be interesting to see whether any considerable invasion occurs about 1930.

The existence of a periodicity apparently corresponding to that of the sunspot cycles suggests that climatic factors have to do with the causation of the phenomenon. It would seem possible that these might operate in either of two ways. A series of favourable years may have the cumulative effect of producing actual overpopulation: or an unfavourable year may have the effect of producing adverse conditions and thus relative overpopulation—frosts and heavy snow in spring, making the birds' food inaccessible, have indeed been stated to be the cause. In either case there is a presumptive stimulus to range-expansion. (The climatic cycles which are related to the periodicity of sunspot

maxima and minima, and the biological influence of these cycles, have already been discussed in the Introduction to this book.)

The Rose-Coloured Starling

On a much less remarkable scale, but in some respects similar, are the occasional irruptions of the Rose-coloured Starling (*Pastor roseus*). This species is native to south-eastern Europe and to western Central Asia, while in winter it reaches India and Ceylon and has been recorded in northern Africa. At irregular intervals flocks visit Western and Northern Europe, including the British Isles. These visitations generally occur between May and October but the species has not bred in this country. It appears that even the ordinary distribution is variable and uncertain. (Records for 1908, for the whole of Europe, have been put together by Von Tschusi.)

The Crossbill

A different case is that of the Crossbill (*Loxia curvirostra curvirostra*), a northern species which migrates southwards in large numbers in some years. There is a resident subspecies (*L. c. scotica*) in the wooded regions of the Scottish Highlands, but the typical form is probably not indigenous to the British Isles. At intervals of a few years irruptions into this country occur in the late summer, after the close of the very early breeding season, and some of the birds remain to breed in the following year or years, although except in Ireland they have not become permanently established here.

Small numbers of immigrants are observed every year, and the greater irruptions seem to occur, on an average, about once in seven or eight years : seasons in which they have been recorded are 1838, 1855, 1863, 1867, 1887, 1894, 1898, 1903 and 1909. According to Ussher the permanent colonisation of Ireland as a new breeding area dates from the irruption of 1838, but has increased in extent after subsequent invasions, notably after that of 1887.

The irruption of Crossbills into the British Isles which took place in 1909 was noteworthy both as regards the large numbers of birds taking part and the wide spread over the country. Its progress was studied and put on record by Lynes, by Eagle Clarke, and by Witherby and Alexander. The first record was from Fair Isle on 23rd June, and the

next earliest records were chiefly from the east coast of Great Britain. Afterwards many of the northern arrivals moved southwards, but there was also apparently a direct immigration to the English coast. Eventually the birds were most abundant in the south-eastern counties, up to a line drawn from the Wash to Portland Bill: a few were recorded from Wales and from some parts of Ireland. In the southern and eastern parts of England some of the birds remained through the winter and bred in the following spring, the first nest on this occasion being found in Norfolk on 12th January, 1910—already with nestlings. The breeding season extended to May, but most nests were found in March and April: many of the birds, however, remained in flocks without breeding. By October, 1910, most of the birds had left.

The Waxwing

The irruptions of the Waxwing (*Bombycilla garrulus*) take place in winter. The breeding range of the species extends from northern Scandinavia eastwards through northern Russia and Siberia to western North America. There is a normal migration every year which extends to Central Europe but scarcely touches the British Isles. In some winters, however, much greater movements occur and large numbers of the birds appear in the British Isles. There is a record of an invasion of this kind for as long ago as 1686. More recent winters in which the Waxwing has appeared in large numbers in the British Isles, where it is otherwise a rarity, have been 1830–1, 1834–5, 1849–50, 1866–7, 1872–3, 1892–3, 1903–4, 1913–14 and 1921–2. The records of the occurrences of the species on these occasions are well distributed over the whole of the British Isles, but most are for the more northerly and easterly districts. They are chiefly for the winter months, but sometimes for as early as August and on the spring passage for as late as May. It will be noticed that the invasions recorded since 1830 have occurred at intervals of from four to twenty years, the average period being 11·5 years.

The records for the most recent irruption have been analysed by Ritchie, particularly as regards Scotland, from where the largest number of the British records came on this occasion. Two birds were noted at Dartmouth on 25th September, 1921, some time before the main invasion began. On 10th November Waxwings were recorded from a number of places in Scotland and from Lancashire, and

in the next few days further records were added. The vanguard was followed on 16th November by still larger numbers and a wide extension of the area visited became apparent, the dates revealing an inward spread from the eastern seaboard. The evidence goes to show that fresh arrivals continued until the early days of December, culminating then in a final wave. It is probable that the heaviest arrivals were on the east coast of southern Scotland, with flanking movements on both sides, but especially on the northward one. The records account for about a thousand birds, but from this total all overlapping cannot have been eliminated: on the other hand, other birds doubtless passed unrecorded. The birds that were not killed or captured apparently passed on farther to the southwards, for relatively few were recorded after January, 1922, and only at one place in Scotland, although some remained in England until early April.

Ritchie, whose careful summary has been followed above, concludes that scarcity of food was the prime cause of the movement towards the British Isles, for the summer of 1921 was apparently notorious in Norway for its lack of wild berries. The normal autumn movement of the Waxwing appears to be less a definite migration than a gradual but limited southward wandering in search of this particular form of food: in 1921 the flocks reaching southern Norway are presumed to have been compelled by the scarcity of food to hasten and extend their usual movements. Ritchie has also compared the migration dates with the meteorological conditions prevailing in southern Norway. He finds that the whole of the period of migration south-westwards across the North Sea was one of high barometric pressure, a condition known to predispose to migration (see previous chapter), and that each of the three principal waves of migration, reaching a climax respectively about 10th November, 18th November, and 4th December, was preceded by a sharp upward fluctuation in pressure. Further, he thinks that the easterly winds prevailing at these times may perhaps have influenced the direction of flight, and so brought the movement to the British Isles.

Other Examples

The Mealy Redpoll (*Carduelis linaria linaria*) is a northern species which is an irregular autumn and winter visitor to the British Isles, particularly to the northern isles of Scot-

land and to the northern part of the eastern seaboard of Great Britain, and is more rarely recorded in spring. In some seasons immigration from the north takes place on a large scale, as in the years 1829, 1847, 1855, 1861, 1863, 1873, 1885, 1897, and 1910—that is, about once in ten years on an average. Evans has given some account of the 1910 invasion in Scotland.

The Siberian race of the Nutcracker (*Nucifraga caryocatactes macrorhynchus*) spreads over Europe in winter in some years and is rare or absent in others. Large invasions were recorded in 1844, 1864, 1885, 1896, and 1907: Elton describes the period as being one of ten to eleven or twenty to twenty-two years, and quotes Simroth as having drawn attention to the correlation with the sunspot cycle. Simroth's conclusion, however, has been criticised by Schuster on the ground that the dates he has taken as those of the principal invasions have only a restricted local validity. The irruptions scarcely affect the British Isles, and of the relatively small number of birds which have been recorded here many have not been distinguished with certainty from the European race (*N. c. caryocatactes*), examples of which also occasionally wander to our coasts.

Apparently as the result of tempestuous conditions at sea, great visitations of the Little Auk (*Alle alle*) to the British coasts take place in some winters, such as those of 1894–5 and 1911–12. Many birds are then found dead on our shores, particularly in the north and east, whereas ordinarily the species does not come under notice in large numbers.

This short account of a few examples of irregular migrants, the chief ones affecting the British area and north-western Europe generally, must suffice for the present purpose. The subject is one of much theoretical interest, and will be referred to again, because these irregular movements might conceivably be regular migrations in the making: from that point of view they are all the more worthy of special study.

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PART II

SOME SPECIAL STUDIES OF BIRD-MIGRATION

WITH PARTICULAR REFERENCE TO THE RESULTS OF BIRD-MARKING

"But then we must not, I think, deny migration in general; because migration certainly subsists in some places, as my brother in Andalusia has fully informed me. Of the motions of these birds he has ocular demonstration. . . . At present I do not know anybody near the seaside that will take the trouble to remark at what time of the moon woodcocks first come; if I lived near the sea myself, I would soon tell you more of the matter."

GILBERT WHITE, Letter to Daines Barrington, 1771.

CHAPTER VIII

OBSERVATIONAL METHODS FOR THE STUDY OF MIGRATION

"As the beacon-blaze allures
The bird of passage, till he madly strikes
Against it, and beats out his weary life."

TENNYSON, " Enoch Arden."

Individual observations—In inland districts—In coastal districts—Local studies of migratory status—Observations at islands and other special stations—Lighthouses and lightships—Collective observations—The British Association inquiry—The British Ornithologists' Club inquiry—Other investigations—The seasonal distribution of geographical races—The study of behaviour.

INDIVIDUAL observation of bird-migration is of course largely dependent for its success upon the opportunities which the observer's station provides. In an ordinary inland district, as has already been noted, it is often the case that little more can be observed than the seasonal appearances and disappearances of different species. With frequent and accurate observation it is possible to note fluctuations in numbers and so to gauge the progress of influx and exodus, and also to learn something of the movements of those species which are represented throughout the year. The flocking which in some cases precedes the departure of summer visitors can also be noted, but only occasionally will anything be seen by day or heard by night of migration actually in progress.

On the coast the observer may see more of the movements themselves, and when he sees land birds coming in over the sea he may be tolerably sure that he is witnessing migration, and not merely some slight movement which forms part of the ordinary routine of the birds' daily life. But unless the conditions at his station be peculiarly favourable, the migratory events which he will see will be so relatively few that he will have little data from which to construct any picture of the whole of the great movements taking place.

Despite the difficulties of observation it would be a mistake to depreciate the value of the information which can be obtained by careful study. It is possible at least

to assess the local status of each species, and much valuable information of this kind is to be found in the more modern works dealing with the avifauna of particular districts: of local studies of this kind dealing with regions of the British Isles, some examples have already been named in Chapter II.

Even the bare recording, from year to year, of the dates of first arrival of different summer visitant species in a particular locality may have its value, and mention may be made of the interesting series of records made in Norfolk by members of the Marsham family over the greater part of two centuries, and partially published at various times (*vide* Southwell).

A method of studying the arrival of summer visitors more closely has been described by C. J. and H. G. Alexander. These observers took advantage of the fact that in the case of many species, during the breeding season, each pair inhabits a definite territory, into which others do not intrude. They therefore took a limited area—eight square miles were worked in one investigation—and on a large scale map recorded the localities of breeding pairs of all species of birds. In the following season they were able to note the dates on which the different territories were taken up: only a few birds were noted which appeared at a place one day and were gone the next, being obviously migrants on their way to a farther destination. It was found that arrivals came in "waves," each apparently dropping a few individuals of a species in the district: thus the filling of the district with its complement of any one species took several weeks, although the males inhabiting some particular small tract, such as wood or stream valley, often appeared to arrive together. Censuses of this kind are of interest from other points of view as well, and the method is one which might prove of much value in the hands of further observers having the necessary opportunities for the very close watching which is required.

Records of first arrival give only a partial indication of the time of a movement. The date of first arrival in any numbers is perhaps more important, as excluding merely stray individuals, and after that there will be one or more dates of maximum influx marking the culminating point or points of the immigration. There is also the date of last arrival, finally completing the movement. For comparative purposes one may wish to take the middle date of the movement, or a mean date may even be calculated if it is possible

to assign a numerical value to the immigration on each day of the movement, although it is seldom that an immigratory movement is not complicated by an overlapping passage movement to regions beyond. In any event, precision of this kind can but rarely be possible for the observer in any ordinary district.

There are, however, favoured spots at which the single observer can really see a great deal of migration, or can at least obtain much indirect evidence of its progress. These stations are for the most part small islands situated in the paths of important migration streams and resorted to for temporary rest by large numbers of the travelling birds. On such an island the observer may perhaps see little more of actual migration flight than he would on the coast of the mainland, but his opportunities for indirect observations are of a quite different order. In many cases the island will have only a small bird population of its own, restricted also as regards variety, and it may afford little cover for the resting migrants which will on occasion be concentrated within the small area of available land. It may thus be possible for the observer to make a complete census of the birds on his island every day, and so to learn much of comings and goings of which he may perhaps actually see no more than an observer on the mainland in the case of similar movements there. In a mainland district observations of this kind are as a rule impossible: there will be a large and varied native population of birds, and there will probably be abundant cover of different kinds which will make exhaustive search very difficult. There will, moreover, be less concentration of resting migrants, and no limits to the area to be searched. The observer may, of course, select some limited area for intensive study, but the boundaries of this will be arbitrary, and the new birds which he sees may have come from only a mile or so away and next day may disappear from his ken by a flight of no greater importance. On an isolated island, on the other hand, the observer searches the whole of the land which exists in a wide area, and every appearance and disappearance of birds from day to day necessarily betokens migration.

It was the opportunities of this kind, utilised for a lifetime, that enabled Gätke to make the island of Heligoland so justly famous in the annals of ornithology. Lying off the mouth of the Elbe and some 27 English miles from the nearest land, this island consists of a flat green-topped

table of bright red rock. The cliffs are 200 feet in height, and at high tide the waves dash right against their base except on one side, where a little low ground is the site of part of the town, and is called the Unterland, the remaining houses being perched on the Oberland above. The island is about a mile long and triangular in shape, the narrow northward end being open grassland for the most part. There is no cover for birds except in the bushes of a few small gardens and in the patches of growing potatoes. A small sandy islet a mile or two away, known as the Dune, completes the picture.

An example of the advantages of Heligoland as an ornithological station occurred during the first twenty-four hours of a visit made to it by the present writer in the autumn of 1908. On the afternoon of our arrival we walked round the island, thoroughly searching the open part of the Oberland. This we found to be teeming with Wheatears (*Œnanthe œnanthe*), which rose from the grass at every few steps. There must have been about two hundred in all, although almost no other birds were seen. Next morning there were not more than two or three dozen, and in searching Heligoland we were searching all the dry land within a radius of about thirty miles. In a mainland country district of that size two hundred Wheatears might rest for a day unnoticed. But even if they did not disperse, and were therefore observed, a negative observation on the following day would not decide whether they had merely travelled half a mile or dispersed slightly, or whether they had really migrated, as we knew our Heligoland birds had done.

Although Heligoland is the classical example of an island observatory it is in no way unique, as the more recent observations of Eagle Clarke on Fair Isle and elsewhere have proved. Fair Isle lies almost exactly midway in the 50-mile gap between the Orkney and Shetland groups. It measures something less than three miles from north to south, with an average breadth of one mile, and its highest point is 712 feet above sea-level. The coast-line of the island is greatly indented, and except at a few points it consists of a line of precipices of which some are nearly 600 feet high. The inhabitants are crofter fishermen, and the southern part of the island is under cultivation: the rest is mostly barren, and nowhere are there trees or shrubs of any kind. At each end there is a lighthouse.

This, then, was the place selected by Eagle Clarke as a

bird observatory, and his forecast of its importance has been more than fulfilled. " Indeed," as he says, " it has become the British Heligoland. Quite a number of species which were previously regarded as rare casual visitors to our isles, have, as the result of these observations, been found to be regular migrants. They doubtless occur on the mainland, too, but owing to its broad acres they almost entirely escape notice. In addition, several species have been added to the British and many to the Scottish avifauna through the Fair Isle investigations. . . . This insignificant island has been visited by no less than 207 species, or *about one-half of the birds that have ever been known to have occurred in the British Isles!*" And since the quoted passage was written still further results of great value have been obtained.

Birds may be seen by day arriving at, leaving or passing the island, and at night the lighthouses contribute their opportunities for observation. The great value of the station, however, lies in the concentration of resting migrants during the day, especially on the cultivated land where cover is available : the many birds which rest on the faces of the cliffs are unfortunately much less easily brought within the scope of observation.

Other island observatories that have been made fruitful through the labours of the same authority are the Flannans, west of the Hebrides ; St. Kilda, still farther out in the Atlantic ; Sule Skerry, west of the Orkneys ; and Ushant, off the coast of Brittany. Mention may also be made of the work of Baxter and Rintoul on the Isle of May, in the Firth of Forth. Promontories, such as Spurn Head in Yorkshire and Blakeney Point in Norfolk, have also been found to possess many of the advantages of island stations.

While the observations of Gätke on Heligoland have, after an interval, been continued by Weigold and others, the German Ornithological Society has for many years now maintained, under the direction of Thienemann, an observatory at Rossitten, in East Prussia, a station which is not an island but possesses advantages of a similar kind. At the south-eastern corner of the Baltic Sea there is a large lagoon, the Kurisches Haff, into which flow the waters of the Niemen and other streams. The lagoon is about sixty miles in length parallel to the coast, and about twenty miles in greatest breadth. It is separated from the sea by a long narrow peninsula, the Kurische Nehrung, leaving only a small outlet at the northern end. The Nehrung

varies in width from about half a mile to about two miles, and for great parts of its length it consists largely of sand-dunes, some of which rise to a height of almost 250 feet. Here and there, where the peninsula is relatively wide, there are small villages with patches of cultivation and woodland, and the menacing dunes are to some extent kept anchored by palisades and by afforestation. If Rossitten is not an island it is at least an oasis, for where its surroundings are not water they are a wilderness of inhospitable sand. It lies in the path of important migration streams, and not only does it possess advantages of search scarcely inferior to those of an island, but it is a place from which vast diurnal movements are seen in actual progress. In a previous chapter a description of one such movement, seen by the writer, has been given.

For individual observation, especially of nocturnal movements in progress, lighthouses and lightships have special advantages to which reference has already been made. Observations of this kind have been made by Eagle Clarke at such places as the Eddystone Lighthouse in the English Channel and the Kentish Knock Lightship off the Thames estuary, by Patten at Irish lighthouses, and by others. The ideal station is, of course, an island which possesses a lighthouse, so that the two kinds of observation may be combined, and this is the case on Heligoland, Fair Isle, the Isle of May, and elsewhere.

So far, only the possibilities of individual observation have been considered here, and the question of collective observation—the systematic co-ordination of the efforts of a large number of observers distributed at different stations over a wide area—may now be discussed. Investigation on these lines dates back to 1855, when Middendorff analysed the data for the arrival of summer visitant species in European Russia. His method was to plot out "isepipteses," or isochronal lines, joining up all localities corresponding with each other as to their average dates for the arrival of particular summer visitors. This mapping of lines of ornithological latitude, so to speak, provided a basis for theoretical deductions which need not now be considered here. The method was employed subsequently by others in different parts of Europe, and it has more recently, for example, proved of value in the hands of Schenk and his colleagues in Hungary. Thus, on the basis of records collected over many years as to the average dates of the spring arrival of the Woodcock in various parts of Hungary, Schenk has shown that the first

arrivals are noted in the south-west and the last in the north-east: the direction of the immigration is therefore believed to be north-easterly from the Adriatic region. It should be noted, however, that the method cannot be successfully applied to a small area: on a detailed scale the records will usually fail to show a regular series of advancing waves, records for the more distant localities often preceding those for nearer ones.

Probably the most important collective investigation ever attempted was that initiated by a special committee of the British Association for the Advancement of Science appointed in 1880 as the result of preliminary work by Harvie-Brown and Cordeaux. Over a period of years observations were made by the keepers at light-stations all round the British coasts, and published in a series of annual reports. The great mass of data collected in this way was afterwards analysed by Eagle Clarke, his conclusions being published in the Committee's final reports, and at a later date in collected form with other matter in his well-known book (1912). It is largely on account of this valuable piece of work that the movements of migratory birds in the British area are so relatively well known, and the information so gained is the principal basis of the summary given in the second chapter of the present book. Similar investigations of less extent have been made by Barrington at Irish lights, by Winge at Danish lights, by Blasius at German lights, and also in America.

The British Association inquiry was largely restricted to observations at lighthouses and lightships. It has since, however, been supplemented by a later investigation conducted for ten years by a committee of the British Ornithologists' Club, under the chairmanship of Penrose, in which, in addition to some light-station observations, the help of observers scattered throughout England and Wales was obtained. Nine annual reports have been published, but an analysis covering the whole period is as yet lacking. In Scotland a good deal of information of a similar kind has been embodied in the annual ornithological reports formerly compiled by Paterson and more recently by Baxter and Rintoul.

Abroad, systematic collective observations have been made at various times and places, notably in Hungary by the Royal Hungarian Institute of Ornithology, and by Bretscher in Switzerland. In America the Bureau of Biological Survey attached to the U.S. Department of

Agriculture has published bulletins by Cooke and others summarising the available data relating to the seasonal distribution and migration movements of different species. The conditions in the United States are distinctly favourable to concerted investigations of this kind, it may be noted. The whole width of the continent from ocean to ocean, through twenty degrees of latitude, is the territory of a single nation, and to the north lies still more land where the same language is spoken: the investigator has thus an opportunity of organising observations on a great scale. In Europe, on the other hand, purely national schemes cover too little ground, and international co-operation is difficult to achieve: in the southern countries, too, there are very few observers to be found, while on the east there is an arbitrary limit to schemes of research instead of the natural boundary of ocean. The method of plotting average dates in isochronal lines, already referred to, has been used in America, by Cooke, with advantage. By this means he has shown, for instance, how the immigratory tide, in the case of several species of summer visitors, flows earlier on the Pacific slope than in the central and eastern regions.

One other aspect of collective investigations may be mentioned in conclusion. In many species the ornithologist of to-day recognises a number of component sub-species or geographical races, each of which has its particular distribution. Much could be learnt, as Meinertzhagen has urged, by the working out of the winter and passage distributions of these separate races in addition to their breeding ranges. Valuable information would certainly accrue as to the broad relationship between particular summer areas and particular winter areas. The determination of the winter and passage distributions of geographical races is, of course, more difficult than the determination of their breeding ranges: in the latter case a large degree of segregation may be assumed, while in the former great overlapping may, and often does, occur. Unfortunately the distinctions of race are not as a rule such as can be accurately determined by the field observer, and it is therefore to the labours of systematic ornithologists that one must look for further light on this part of the subject. This increases the need, as Meinertzhagen points out, for adequate field data with all specimens reported on: collecting will be barren indeed if it is done in such a way that nothing is added to our knowledge of the living bird.

This chapter must not be concluded without reference to a rather different kind of observation which is also worthy of attention. Here the subject has been dealt with from the point of view of the study of the movements which occur, but in his last and posthumously published book Hudson puts forward a special plea for the study of the behaviour of individual birds before, during and after migration flight. The subject is certainly of importance as well as of fascinating interest, but Hudson appears to have overstated the case gravely when he spoke of this kind of observation as the only one likely to lead to a better understanding of the inner meaning of migration. The behaviour of the migrants must not be neglected, but a knowledge of the nature and extent of their performance is surely at least as necessary, and to this author's rather careless remark—he had no opportunity of revising his manuscript—that other methods of study have failed, one must reply that these methods have not as yet been fully exploited and that they have already added immensely to our knowledge.

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CHAPTER IX

THE METHOD OF BIRD-MARKING FOR THE STUDY OF MIGRATION

The essentials of the method—Aims of bird-marking—No injury to birds—History of bird-marking investigations in different countries—Methods employed.

As distinct from purely observational methods of study there is the modern method of bird-marking, to which special attention is being given in this book. It has been called the experimental method, but this description is scarcely warranted: there is no interference with the course of Nature, and no artificial control of the conditions—marking is, rather, a special kind of aid to observation.

In its essentials the method consists of the marking of a large number of birds, in some way or other, for the sake of the data afforded by the subsequent reappearance of a few of them. The principle is identical with that of the well-known method of marking fishes as a means of studying their movements and life-histories, while an analogous system has also been frequently utilised in the study of ocean currents.

The method differs from other methods of studying migration in that it approaches the subject from the individual aspect—it begins with individual birds and works from them towards general movements. A marking record implies that there are two or more times in the life of a particular bird when one is able to state with certainty its whereabouts and various other facts, these times being commonly those of infancy and death. When a large number of these records has been collected and correlated, there becomes available an array of facts which could not have been ascertained by other means.

Without at the moment discussing such questions at length, it may be noted how the proof or disproof of many theories of migration must necessarily rest on a knowledge of the facts concerning the relation of particular summer quarters to the corresponding winter quarters, and of the

routes connecting them. Thus it is often suggested in the case of one species or another, that the birds summering farthest north winter farthest south, and that those living midway are more or less stationary ; but the observer only sees a general southward movement, and typical individuals must be singled out for study before the question can be answered. For example, there are many cases of species which are found all the year round in the British Isles, but yet are known in autumn both as immigrants from the north and as emigrants to the south, and *vice versa* in spring. Now, except by marking one can hardly hope to be sure whether it is our own summer birds that emigrate, leaving the new-comers to occupy the area for the winter, or whether our own birds are resident while the immigrants pass on over their heads and journey farther southwards. And until this is known, very little of the true nature of migration can be understood.

Some of the questions which may be answered in due course by the marking method are as follows, and most of them have an important bearing on one or other unsolved problem of bird-migration : To what extent do birds return to their birth-places to breed, and under what circumstances are new areas colonised ? Do birds have definite winter quarters, and if so, do they seek them year after year ? Do young birds seek the same winter quarters as their parents ? To what extent do the birds of a single species native to the same summer area seek the same winter area ? What relation do the winter quarters of the northerly breeding members of a species bear to those of the southerly breeding members ? Are definite paths followed by migrants, and if so, what is their nature ? And these questions by no means exhaust the subject.

Various kinds of marks have been tried or suggested, such as parchment tied under the tail with silk, thin metal discs glued to the tail-feathers, and indelible stamps on the tail-feathers. But all these, besides being clumsy, have the great disadvantage of lasting only until the next moult, and both for convenience and for permanence marks on the feet are obviously the best. In early, isolated attempts at marking, such crude means as brass wire or silk thread twisted round the bird's foot were used ; but in order to allow of an inscription, a broad metal ring is necessary. As combining extreme lightness with a high degree of durability, aluminium is to be preferred, and all the more because it is easily worked and stamped.

Complete rings, such as are used for homing-pigeons, are of little use for marking wild birds, as they can be placed only on very young birds; and not even then in the case of birds with nidifugous young, these having well-grown feet at an early age. Furthermore, these rings are expensive, as they are cut from aluminium tubing instead of from sheet aluminium, and have to be stamped when in circular shape instead of on the flat. Hence the superiority in every way of the "split ring," which is a band stamped from a sheet and then folded into a circle. The edges are merely pressed together, and a ring of this kind, if of small diameter, will keep its shape without difficulty. Rings of larger size must either be of thicker metal to do this, or must have a clasp of some kind. A very simple pattern is one in which the band is longer, and is not all used in forming the circle; two unequal ends are left to project outwards side by side at the meeting place, the longer being afterwards folded over the shorter, and so forming a clasp which, especially if subjected to pressure with a pair of pliers, will effectually prevent the ring from coming off. It may be mentioned that for Moorhens, Divers, and some other water-birds, the rings require to be bent into oval shape to fit the much compressed tarso-metatarsus.

Birds may be obtained for marking in two ways. Either they may be marked as young birds still unable to fly, or they may, when older, be trapped by any non-hurtful means and then marked and released. Notification of their subsequent death or recapture depends on the address which is stamped on the ring. Some markers have been content with mere initials, but this is very wasteful as it is obvious that it must greatly reduce the number of recorded reappearances and practically exclude the possibility of records from any great distance. Many rings with various insufficient addresses have, indeed, been found on birds but never traced to their origin although widely advertised in ornithological periodicals: and there is, in any event, no great difficulty in stamping a short address even on the smallest ring. In addition to the address each ring should bear its own identification number, which is indeed the key to the whole method. Some markers have used year marks (the year in figures, or some arbitrary sign), but this is only possible where the marking is confined to a single locality and to a single species, and if all the birds are marked when they are young. Thus, if the rings bearing a certain address are being used solely for young Woodcock on a

single estate, a year mark is sufficient; but where the histories of the birds marked differ from each other, separate identification is necessary. Species is not a reliable factor for this purpose, in that marked birds are often reported by persons ignorant of the subject, and it is thus essential that the number on the ring should be all that the marker requires in order to determine the species and history of any marked bird of his that is reported.

The rings soon lose their brightness, especially in the case of water-birds, and are not usually visible on the birds except with strong field-glasses and under specially favourable conditions. Marking is thus in no way an encouragement to the killing of wild birds: the proportion of ringed individuals to the whole bird population will always remain so small that any shooting of birds for the chance of ringed specimens would be ridiculous. It is also worthy of note that many marked birds are reported as found dead or wounded, or as captured and subsequently released, while those reported as killed by the finder belong chiefly to the species which are shot for sport.

Various attempts have been made, however, to make ringed birds more conspicuous, in order to increase the proportion of records, by adding bright colours artificially to parts of their plumage. This has usually been found unsatisfactory owing to the rapid disappearance of the colour, but Drost, who has recently taken over the ornithological work on Heligoland, has now found colours which are apparently "fast," and he is exploiting the method by this means. Proper identification rings are, of course, placed on the birds at the same time. It may be noted that the method is inapplicable to young birds, or indeed to any birds which will shortly undergo plumage changes. In dealing with results statistically, also, careful allowance will have to be made for the bias in favour of the occurrence of recovery records in the period between the time of marking and the time of the next moult.

The question as to whether the rings have a harmful or disturbing effect on the birds has also been raised. It must be remembered, however, that the ring rests lightly on the insensitive scales of the foot, and is insignificant in weight compared with the size of the bird; the writer's smallest ring, suitable for Sparrows, weighed only $\frac{1}{6}$th of a gramme, and his largest, for Herons, only about 1 gramme. A newly marked bird pays little or no attention to the ring, and out of a large number of ringed feet returned to the

writer for examination, after intervals ranging from a few days to nearly twelve years, only two or three showed any sign of injury, due in these cases to the use of a wrong size of ring by the marker. It seems desirable to repeat this here in view of the assertions, unsupported by evidence, which have been made to the contrary from time to time. One such case has been discussed by the present writer in a paper with Galloway dealing with the heavy mortality which occurs in some seasons among the young of the Common Tern, the suggestion having been made with some publicity that a connection was to be found between the heavy mortality which occurred one year in a particular colony and the activities of bird-markers at that place. Similar heavy mortality figures were recorded from other colonies where no marking was in progress and from the same colony in certain years prior to the date of marking, and good seasons were reported in other years when marking was done to as great an extent as in the bad one. Obviously there is no connection between the two sets of facts, and other causes are accountable for the heavy death rolls.

That the ring might lead to abnormality in behaviour also seems highly improbable. Migration might presumably be interfered with in cases where a large mass of weeds or other matter became firmly entangled with the ring—no case of this kind has come to the writer's notice—but undue stress can, in any event, never be laid on any isolated record.

The possibility that particular methods of trapping may cause injury is, of course, an entirely different question, and one which depends solely on the suitability of the means employed. Any hurtful method would have to be condemned not only for its cruelty but also as a possible source of fallacy in the results obtained. It should always, however, be quite possible to secure that only means which are not hurtful be adopted.

That trapping can be done without injury to bird-life is shown by the large numbers of birds recorded again, often many times in a single case, in the same traps. Birds of many species, indeed, readily acquire " the trap habit " and become accustomed to handling : they may be caught several times in a day, and may be seen to fly straight back to the food in the trap after being caught and examined. Baldwin remarks that a trapping station becomes a bird sanctuary : food and protection are provided, and a very noticeable concentration of birds on the estate takes place.

Historical Survey

The device of marking birds in some way was not infrequently resorted to, in isolated cases and for special purposes, by naturalists of earlier days, and one often comes across stray records. But it was apparently not until 1890 that the first systematic scheme was set on foot. In that and many subsequent summers, numbers of young Woodcock (*Scolopax rusticola*) were marked by Percy on the Duke of Northumberland's estate at Alnwick. The rings were inscribed with an " N " and the year.

In 1899, Mortensen started a more ambitious inquiry in Denmark; and the Stork (*Ciconia ciconia*), the Heron (*Ardea cinerea*), the Teal (*Anas crecca*), the Pintail (*Anas acuta*) and the Starling (*Sturnus vulgaris*), are among the species which he has studied by this method. This investigator may, indeed, be regarded as the pioneer of scientific bird-marking, because his inquiry was the first which was thoroughly comprehensive in scope and exact in methods: the use of identification numbers instead of mere year figures was a good innovation which opened up many fresh possibilities, although involving much more labour in the way of record keeping. More recently the work in Denmark has been continued by Skovgaard at Viborg, and by Pedersen at Fredericksund.

In 1903 the method was adopted in Germany, an important inquiry being started by Thienemann from the German Ornithological Society's station at Rossitten on the Baltic coast. Results of great interest have been obtained for the Stork, the Hooded Crow (*Corvus cornix*), Black-headed Gull (*Larus ridibundus*), and other species. Subsequently, the work was extended to Heligoland by Weigold and to Bavaria by Stresemann, and the co-operation of the Forestry Service in the marking of birds-of-prey still further increased the scope of the investigations in Germany.

Bird-marking was begun in Hungary soon after the adoption of the method in Germany, and under Herman and Schenk the scheme of the Hungarian Institute of Ornithology has achieved valuable results, notably in the case of the White Stork.

Meanwhile some progress had been made in this country. In 1907 Harvie-Brown recorded that Tomlinson had for some time been marking Starlings at Musselburgh, near Edinburgh. In 1904, Gurney marked a number of young Gannets (*Sula bassana*) on the Bass Rock, Firth of Forth,

with rings inscribed " Bass Rock 1904." In 1905, Hamilton, at Baron's Court, Co. Tyrone, Ireland, began marking Woodcock with rings inscribed with " B.C." and the year in figures. Between 1910 and 1916 over 300 Woodcock were marked by Ashley in County Sligo, Ireland, as reported by Douglas. Other proprietors have also marked Woodcock, for instance, Ardilaun at Cong, Co. Galway, Ireland, using rings inscribed " A., Cong," and Graham has used rings inscribed " R.G." for various species of Duck (for the most part hand-reared) marked at Netherby, Cumberland. In 1908, Ticehurst, following Mortensen's methods, began marking various birds in the south of England with rings marked " Ticehurst, Tenterden." Rings were also issued at that time by the newspaper *Country Life*. Various inquiries on a smaller scale have been set on foot at different times.

In 1909, the first efforts were made at bird-marking on a large scale in the British Isles, two inquiries being started independently and almost simultaneously, namely, the Aberdeen University Inquiry managed by the present writer, and Witherby's scheme in connection with his magazine *British Birds*. The former investigation has been concluded and the results published by the writer (1921). The *British Birds* inquiry is still in progress; and further results continue to be added to those already published by Witherby and others associated with him, among whom the present writer is grateful for being included.

At various dates since 1909 many different marking inquiries have been set on foot in other European countries, including the following: by Stoll in what is now Latvia, and more recently by Piiper in Esthonia; by Rössler at Agram, in what is now a part of Jugo-Slavia; by Hess and others in Switzerland: by Jägerskiöld, and afterwards by Lönnberg and Rendahl, in Sweden; by Tratz in Austria, and by Loos in what is now Czecho-Slovakia; by Palmen in Finland; by Van Oort in Holland; by Menegaux and by Guérin in France; and by Schaanning in Norway. Work in Russia, formerly undertaken by Rossinsky and others, has also been recently revived at Moscow by Koschewnikows.

It was also in 1909 that the efforts of Cole led to the formation of an American Bird Banding Association for the development of the method in the United States, although there had been work by Bartsch and others prior to that date. A few years later the investigations received a fresh impetus from the work of Baldwin, who showed the value

of the study when combined with systematic trapping at particular stations. More recently the responsibility for the organisation of marking in America has been taken by the Bureau of Biological Survey of the U.S. Department of Agriculture, and important results have been published by Lincoln. Bird-marking has also been done in Canada.

Methods

For the sake of example some description may be given of the methods adopted in the Aberdeen University Inquiry. Each ring bore the address "Aberdeen University" (contracted to "Aberdeen Univ." on the smallest size), and an identification number. A plain number, sometimes written in two lines, was used where possible, but on the smallest size the need for brevity led to the use of such numbers as "0798," and letter combinations like "299A." After the first experimental stage the rings were made in the following seven sizes, named in fractions of an inch, the first four for ordinary use and the three largest for those markers who had special facilities for ringing sea-fowl and other large birds. The first three sizes were of the claspless pattern, while the other rings were provided with the form of clasp already described, and had also edges turned outwards as flanges.

$\frac{1}{8}$". Finches, Swallows, Titmice, Redbreast, Lark, Sandpipers, Little Tern, etc.
$\frac{3}{16}$". Thrushes, Starlings, Lapwing, Snipe, etc.
$\frac{1}{4}$". Woodcock, Jackdaw, Black-headed Gull, Kestrel, Teal, Stock-Dove, etc.
$\frac{5}{16}$". Rook, Crows, Owls, Wood-Pigeon, Guillemot, Wigeon, etc.
$\frac{3}{8}$". Herring-Gull, Mallard, etc.
$\frac{1}{2}$". Gannet, etc.
$\frac{5}{8}$". Heron.

The numbers, sizes and destinations of all rings issued to markers were noted, and reappearances of marked birds were checked by these notes. Together with the rings were issued schedules on which the data about all birds marked were to be filled in, the following information being asked for: (1) Number on ring; (2) Species of bird; (3) Date of marking and release; (4) Locality of marking and release; (5) How obtained ("as young," etc.); (6) Sex and age so far as certain; and any other remarks, including bracketing

together members of the same brood with word to that effect. When the completed schedules were returned, the data were transcribed into ledgers, in which the entries were arranged serially according to the ring numbers, a final column being left blank for the purpose of entering references to the "Case numbers" in the separate card-index of reappearance records. (The ledger system has some advantages, but others have adopted the convenient method of keeping all the particulars on cards which are filled in by the marker.)

When a marked bird was reported as killed or recaptured, the number on the ring was the chief thing required, together with a note of the locality and date of the occurrence. If the ring, with or without the foot, were sent, or if the species were identified, an additional check on the accuracy of the record was provided. Many birds were, naturally, recorded from the places where they were marked, and the interest of these records depended on the lapse of time and on the other circumstances of the case: cognisance was taken of all records of this kind, however, except when a bird was recorded on the same day, or, in the case of young birds, within the flightless period. A definite rule on the point is desirable in order to avoid any artificial selection of the data which might introduce a bias into subsequent analysis. Doubtful or obviously inaccurate records must, of course, be excluded or appropriately discounted, and the risk of undetected errors must be allowed for in assessing the value of isolated records.

At the outset of the investigation no restriction was made as to the species of birds which were to be marked, and each co-operator was left to make use of whatever opportunities he might have. These opportunities were for the most part confined to young birds as yet unable to fly, but large numbers of birds were also caught in nets set up for the purpose and a few were caught at lighthouse lanterns or at night on the sea-shore. It was felt that the widest possible scope would provide the fairest test of the value of the method, and even in the case of purely resident species the extent of local movements was considered worthy of study. Earlier schemes, perhaps more by chance than by intention, had been confined for the most part to a limited number of especially interesting species which had well repaid the labour and cost of marking: no guide, therefore, existed as to the possibilities of a more comprehensive plan of campaign. Towards the close of the Aberdeen inquiry an

attempt was made to benefit by experience and to concentrate effort along lines which seemed likely to be most remunerative, and this question will be considered later from the standpoint of bird-marking investigations in general.

The interpretation of results

Only a small proportion of recoveries can be expected from marking. Two or three per cent is a common figure, but the proportion may be less, sometimes much less, than 1 per cent, as for instance in the case of some of the smaller Passerine species. Lapwings have given something over 2 per cent, and the larger Gulls 4 or 5 per cent. Ducks give high figures, and Mortensen's 20 per cent for Pintail is remarkably good when it is considered that most of the reports came from a distance.

Where systematic trapping is carried out the proportion of recoveries may be greatly inflated. Thus, the present writer found that of 898 Hedgesparrows (*Prunella modularis*) marked, 66 were recovered, making 7·3 per cent: but a further analysis showed that of 142 marked at one station, 42 were recovered there, or 29·6 per cent, and of 131 marked at another station 17 were recovered there, or 13·0 per cent, while of the 625 marked elsewhere, without retrapping, only 7 were recovered, or 1·1 per cent. Similarly, in the case of the Blue Titmouse (*Parus cæruleus*) a recovery percentage as high as 90·2 was recorded at one station, although the proportion recovered of birds marked where retrapping was not attempted was again only 1·1 per cent. Systematic trapping also yields numerous "repeat" records for the same bird. Musselman records that a single Chipping Sparrow (*Spizella passerina*) was recaught fifty-four times in one season and fifty-one times in the next.

In interpreting marking results it has thus to be remembered that, apart from systematic retrapping, one is dealing with only a very small proportion of the number of birds marked, and that this proportion may well be not completely representative. Birds are in the first place killed or caught in varying numbers, and in different ways, according to place and season. In the second place the human factor comes in, and the chances of a recovery of a marked bird being reported vary with the region and the attendant circumstances. There are obviously greater chances of recoveries being reported from some places than from others, and in general the results are probably biassed to

some extent in the direction of a disproportionately large number of recoveries from the place or region of origin, and of a deceptively small number from great distances. Where systematic trapping is practised more birds are recovered, but the aforesaid bias is at the same time much increased, as the figures already quoted for the Hedge-sparrow and the Blue Titmouse clearly show.

In other words, the number of birds in a given area at a given time is only imperfectly represented by the mortality and capture rate, because the latter varies with the time of year and other circumstances: and the true mortality and capture rate is perhaps still less adequately represented by the recorded mortality and capture rate which forms the statistical datum of the method, because obviously a smaller proportion of dead marked birds will be reported from some places or countries than from others.

There is virtue, too, in mere numbers of records, as may be seen from the following example (*cf.* Chapter XI). Out of 3142 Lapwings (*Vanellus vanellus*) marked, 62 were recovered, or 2·0 per cent. When the total was split up into groups according to native districts or to years of marking, the separate percentages were found to vary from 0·4 to 3·3 in the groups of 200 or more, and from 1·3 to 2·9 even in those groups containing over 400. Obviously, therefore, no percentage figure can safely be used for comparative purposes unless it is based on a total of many hundreds of marked birds.

Real statistical treatment of marking results, even when these are numerous, is therefore made very difficult. Where the problem takes the form of comparisons between sets of records collected under approximately similar circumstances, however, a quantitative as well as a qualitative significance may perhaps be attached to the data.

It follows from these considerations that much caution is necessary in the interpretation of marking results. In particular, it is important that undue weight should not be given to negative evidence. The absence of records from a particular area or at a particular season is significant only when it can be shown that the species tends to yield a good proportion of records in circumstances such as are prevalent there or then. Failing the fulfilment of this condition, the positive evidence may be taken as a partial representation of the real facts, but it cannot be regarded as a complete representation while the complementary negative evidence is unsatisfactory.

Another point to be noted is that one must avoid making an *a priori* assumption to the effect that birds marked in the same circumstances will behave alike. It does not, for instance, follow that the recovery localities of birds of a given species marked at the same time and place necessarily trace out a path followed in common by the different individuals to the points at which they respectively came under notice: the localities may in reality lie on several different paths, and any contrary assumption begs the very question at issue. This difficulty can be wholly surmounted only when the number of records is sufficient both to make a clear positive case and to permit of the negative evidence being taken as significant.

There would appear to be two broad classes of results which marking may yield: these may be roughly described, respectively, as individual and cumulative. In the first class may be placed records which, repeated a few times, establish a new fact of great interest, but which seem unlikely ever to become sufficiently numerous to afford a basis for detailed analysis. Records of this kind enable one to say that such and such *sometimes* occurs, but for an attack on the fundamental problems of migration one requires data from which it can be inferred that such and such is the rule or occurs to a certain definite extent—records which fit in with many others to give a more complete picture of some particular movement. This second kind of record is to be obtained, whether by special concentration of effort or not, from marking the more "remunerative" species on a large scale and in a systematic manner. Three requirements must, from the outset, obviously be fulfilled by any species before it can be expected to be "remunerative": it must be of interest as a migrant, it must be procurable for marking in large numbers, and it must yield a good percentage of reappearance records: with regard to the last of these points a good deal has now been learnt. There is, however, still another requirement which actual experience of working the method has revealed, namely, that the circumstances must be such as will not invalidate the results by the introduction of too many uncertain factors.

The most satisfactory way of making a detailed analysis of the records for any species seems to be to classify them in homogeneous groups within each of which every record is strictly comparable with the others, and between which some comparison on broad lines can also be made. (An example of the working of this method is given in some

detail, for sake of illustration, in Chapter XI.) The point is a very important one in the British Isles, where, in the case of very many species, a mixed population of natives and visitors is present in winter : when marking is done in winter it thus often becomes difficult to analyse the heterogeneous records without making assumptions which beg the question to be investigated, namely, the differences between the various groups represented.

What is greatly to be desired, therefore, is a large number of records relating to a homogeneous group, and this is obtained at its best when many birds of a single species are marked during the breeding season in a definite area. This condition is fulfilled in many cases, as examples shortly to be given will show. The next step, however, is to compare a series of such groups, for the same species but for various areas. This, unfortunately, is much less easy to achieve, because few species have as yet been marked on a large scale in two or more separate areas.

Next to the marking of birds in summer in their breeding areas, the marking of birds in winter in regions where they are unknown at other seasons seems most likely to give results of special value. The success attending marking on these lines in America is noteworthy, and it is evident that it can yield records of a kind which are seldom to be obtained by other means and which are complementary in a useful way to those given by summer marking. In particular, winter marking under these conditions can give results as to the return to the same or other winter quarters in subsequent seasons, and this can but rarely be shown by summer marking owing to the great chances against any bird being recovered more than once apart from " repeats " at the place of marking.

In interpreting the results of marking in the winter quarters of a species, it has, of course, to be remembered that there may be present birds native to two or more distinct breeding areas. It can, however, at least be postulated that each bird has been absent from the region of marking in the summer or summers intervening between the date of marking and the date of recovery. Where birds are marked in winter in an area where some are resident and some winter visitors, this is obviously not the case : the results will thus not lend themselves to analysis, and only the individual records showing actual movement will be susceptible of proper interpretation.

From a consideration of these various factors, the present

writer has formed the opinion that intensive rather than promiscuous marking will eventually prove most fruitful. This is not to say that promiscuous marking, which has yielded some excellent results, is to be condemned in itself, but only that opportunities for intensive marking should be seized whenever possible. It is for the promoters of any scheme of marking to judge whether, in the circumstances of their work, any attempt at concentration will produce the desired result or lead merely to a restriction of effort. The point is certainly one which is very relevant to the future development of work upon the subject.

In passing, it may be noted that bird-marking may serve other ends than those concerned with the study of migration. There are various kindred points relating to distribution, for instance, and interesting evidence as to longevity and the rate of mortality may be obtained. Furthermore, it might be a valuable aid to the study of plumage sequences to acquire a collection of birds which had lived entirely free and natural lives and of which the ages were accurately known. Burkitt has also described a method for use in a field study of the behaviour of a community of birds in which it was necessary that individuals should be recognisable without repeated capture. For this purpose rings of different colours were used, and by putting several rings on one bird, variously distributed between the right and left feet, a sufficient number of combinations was possible. Interesting studies of habits have also been made in America by Baldwin (1921*b*), although in this case it was not necessary that the birds should be recognisable without capture. The last-named investigator, it may be added, has suggested the possibility that marking, combined with systematic trapping, may find its most fruitful field in the intimate study of the daily life of the individual bird.

In the next five chapters an account will be given of some of the results which bird-marking has already added to the material for the study of bird-migration. It is thought that this will be found to contain more than enough evidence to prove that the method is one of great value for the purpose. It seems important, nevertheless, that the difficulties and limitations of the method as well as its great advantages should be recognised, or else there will be a danger that unjustifiable conclusions may be drawn from its data as the result of too facile interpretation. It is also to be remembered that bird-marking is supplementary to other

methods of study, and that it should not be practised to their exclusion.

REFERENCES

An extensive list of references to bird-marking and its results will be found at the end of Chapter XV. Of these, the following refer particularly to questions of history or methods such as have principally been dealt with above :—

BALDWIN (1919 ; and 1921*b*) ; BURKITT (1924–25) ; COLE (1903 ; and 1922) ; HERMAN (1910) ; GEYR VON SCHWEPPENBURG (1922) ; GALLOWAY and THOMSON (1914) ; DROST (1925) ; LINCOLN (1921*a* ; and 1921*b*) ; LUCANUS (1922, 1923) ; LÜHE (1908) ; SCHENK (1910) ; and THOMSON (1911*a* ; 1921*a* ; and 1921*b*).

CHAPTER X

THE MIGRATIONS OF THE SWALLOW AND OF THE WHITE STORK

The Swallow, with special reference to the British area: Distribution—Spring immigration in Europe—Summary of observed British movements—Behaviour as a migrant—Marking results—Return to the same summer quarters—Migration through Europe—Winter quarters in South Africa—and in West Africa.

The White Stork: Distribution—Marking results—South-easterly autumn migration in Europe and the Mediterranean countries of Asia, and the corresponding spring passage—South-westerly autumn migration in Europe—Possible migration towards the Indian region—Migration and sojourn in Africa—Return to native area—Conclusions.

THE first two species which have here been selected as examples for special study of their migrations are both typical migrants in the sense that they are wholly summer visitors to a wide area, withdrawing entirely from their European breeding range in winter. The study of their migrations in Europe is accordingly uncomplicated by any such factors as the existence there of a proportion of non-migratory individuals, or as an overlapping of the summer and winter ranges within the area.

THE SWALLOW (*Hirundo rustica*)

With special reference to the British Area

In summer the Swallow is found throughout almost the whole of Europe, in western parts of Asia, and in north-western Africa: it has been suspected of breeding in Uganda and on Kilimanjaro. The typical race is replaced by allied forms in Egypt, in parts of Asia (as far as Japan), and in North America. In winter it is absent from its breeding range, except perhaps near its southern extremity, and at that season, according to the cycle of the year in the Northern Hemisphere, it is found in Africa as far as the extreme south, and in India and the outlying islands. In the British Isles it breeds everywhere except in some of the remoter Scottish isles, and it also occurs as a bird of passage on its way to and from its breeding area in Northern Europe.

Sclater states that in South Africa the Swallow first arrives near Cape Town at the end of October, becomes common in November, remains till March, and has entirely disappeared by the middle of April. While some are still lingering in these distant winter quarters, however, others have already arrived in Europe, for, according to Irby, Gibraltar is reached by 13th February. Herman reckons that 105 days are needed for the invasion to spread to the extreme north of the Continent, Luleä, in Sweden in 67° N. lat., not being reached until 29th May, by which time there are already fledged young at Gibraltar. He also quotes Hegyfoky as calculating a delay of 1·17 days for each 100 metres of altitude : thus, Swallows reach a locality in the Carpathian Mountains, about 3300 feet above sea-level, on 5th May, which is 28 days later than the average for the whole of Hungary.

As regards the British Isles, it is possible to give a relatively complete account of the main movements which take place. The data collected by the British Association Migration Committee have been analysed by Eagle Clarke, and his conclusions have been confirmed and supplemented by the subsequent inquiry of the Migration Committee of the British Ornithologists' Club. The facts may here be briefly summarised.

A few early birds may appear in March, but the average times for the arrival of the vanguard of our summer visitant Swallows are : for south-western England the beginning of the first week in April, for Ireland the end of that week, for south-eastern England early in the second week, for south-western Scotland the end of the same, for south-eastern Scotland the middle of the third week, for northern Scotland the fourth week, and for the Orkney Isles the second week of the following month : the main influx usually begins some ten or twelve days later in each case. The earlier dates for the western region, latitude being equal, are noteworthy, and it appears that the immigratory waves arrive along the whole length of the south coast of England, but first and chiefly on its western half. Before this immigration of our native birds has been completed—at the very end of April—there begin the passage movements of Swallows traversing the eastern seaboard of Great Britain *en route* for Northern Europe, and these movements may be prolonged until almost the middle of June.

Decided southerly movements within the British area

begin towards the end of August, and early in September actual cross-channel emigration sets in and continues for nearly two months, after which only stragglers are as a rule recorded. From the middle of September onwards there is also the return passage of Swallows from Northern Europe, and the two sets of movements are not easily distinguishable. There is also a passage movement from Central Europe, first observed by Eagle Clarke from the Kentish Knock Lightship, the line being roughly from east to west ; the existence of a corresponding spring passage on this line has not been definitely established. A few instances are on record of Swallows surviving in this country throughout exceptionally mild winters.

In a previous chapter some account has been given of the migration of the Swallow as it may be seen in progress at a favourable station. The movements are usually diurnal, although notable exceptions have been recorded. The species is, of course, markedly gregarious, and the great " flockings " which precede emigration are familiar to all. Old and young often " flock " and migrate together, but sometimes in separate companies. Occasionally the great flocks migrate *en masse*, but more often in small detachments. Although so notably gregarious among themselves, it is comparatively seldom that Swallows are accompanied on migration by other species, the House-Martin (*Delichon urbica*) being the only frequent exception. A strong migration of Swallows takes the form of a continuous stream of small and scattered bands, usually flying at a very low elevation.

The former knowledge of the migrations of British Swallows, as outlined above, has recently been supplemented by records of marked birds. Under the *British Birds* scheme, 10,744 Swallows had been marked up to the end of 1924 and 73 (0·7 per cent) recovered up to the time of completing the list published in the magazine in December, 1925 : 1,198 were marked under the Aberdeen University scheme, and 5 were recovered (0·4 per cent). The results have added proof that Swallows commonly return to their former summer quarters in subsequent years, and the beginnings of more exact information as to the routes and destinations of our birds after they leave the area for the winter. Of the information under these two headings a summary may be given.

Witherby especially, and the present writer to a lesser extent, have obtained records of marked Swallows returning

to their native districts in the British Isles in subsequent summers. Twenty-one marked as nestlings have been so recorded, seventeen in the following summer, two after two years, and two after three years, the localities ranging from Hampshire to Kincardineshire. Six marked as adults have been similarly recorded, three after one year and three after two years, the localities ranging from Staffordshire to Peeblesshire.

In some of the foregoing cases the return to the same place was very exact—even to the selfsame porch or outhouse. In others the place of recovery was a few miles from the place of marking ; a Swallow marked as a nestling at Beaulieu (Hampshire), for instance, was recovered in the following May at Ringwood, in the same county but 18 miles distant. There are a few additional cases, still to be mentioned, in which Swallows marked as nestlings returned in the following summer to parts of the country rather more widely separated from their respective birthplaces, the distances being from Hampshire to Sussex (30 miles), from Hampshire to Middlesex (70 miles), from Stirlingshire to Yorkshire (170 miles), and from County Kildare to County Armagh (75 miles). Another, marked as a nestling in Ross-shire, was recovered at Glasgow (125 miles) after an interval of nine years.

Similar results have been obtained in other countries, but particularly in Hungary, where Von Sceöts has made an elaborate study of the return of Swallows and House-Martins to their nesting places. He has found them returning with great accuracy in many cases, and has no record of return to other localities outside a radius of 2 kilometres. In one instance a bird used the same nest in six successive seasons. He has also noted that a pair may keep together for three years, while in other cases a new mate is taken for the second brood in a single year. In a similar study in France, on a much smaller scale, d'Abadie has found birds marked as adults returning to the same farm : he lays stress on the absence of records for the return of birds marked as nestlings, but his total figures are quite small and his trapping activities were confined to the single farm.

Witherby has obtained a series of most interesting results under the second heading. There are, to begin with, various records of Swallows marked as nestlings and recovered within a few miles a little later in the season, but these are without special significance. The European stages of migration are indicated by records of birds marked as nestlings and

reported in their first year, as follows: one marked in Lancashire from the Isle of Wight, late in October; one marked in Lancashire from Indre-et-Loire, in the centre of France, in September; one marked in Suffolk from Gironde, south-western France, in September; one marked in Staffordshire from Charente-Inférieure, south-western France, in October; and one marked in Staffordshire from Brittany, in December, but without information as to how long it may have been lying dead before it was discovered. One marked in Lancashire as a nestling was recovered in Vendée, western France, in August of its fourth year. Further, a Swallow marked as a nestling in Staffordshire was recovered at Bilbao, northern Spain, in March of the following year. These records are supplemented by two from continental sources. According to Krüss, a Swallow marked in Schleswig-Holstein was obtained on migration at Bregenz, on the Lake of Constance; another, according to Van Oort, was marked as a nestling in Overijsel, Holland, and was recovered on 1st October of the same year at Tangier, Morocco.

Still more interesting are Witherby's records of Swallows marked in the British Isles and recovered in their winter quarters (during the summer of the Southern Hemisphere) in South Africa. The records are as follows:

Ring Number	Age at Marking	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
B.B. B830	Adult.	6.5.11	Staffordshire, England.	23.12.12	nr. Utrecht, Natal.
B.B. E937	Juv.	27.7.12	Ayrshire, Scotland.	16.3.13	Reit Vallei, Orange Free State.
B.B. 82620	Juv.	3.7.15	Lancashire, England.	6.2.16	nr. Grahamstown, Cape Province.
B.B. JM53	Juv.	19.8.18	Yorkshire, England.	21.2.19	East Griqualand, Cape Province.
B.B. KR87	Juv.	27.6.19	Stirlingshire, Scotland.	28.1.20	Lake Chrissie, Transvaal.
B.B. 5224	Juv.	20.8.21	Berkshire, England.	8.1.22	nr. Jansenville, Cape Province.
B.B. 9623	Juv.	18.8.22	Carmarthenshire, Wales.	14.1.23	Springs, Transvaal.

Witherby has drawn attention to the suggestive fact that all these seven records of his are from the eastern portion of South Africa.

To these records from South Africa must be added one from the Belgian Congo. This bird, B.B. FW39, was marked

as a nestling on 31st July, 1921, near Cardiff, Wales, and found by a native in December, 1922, in the upper eastern corner of Luozi district, Belgian Congo, about 4°5′S. lat. and 14°15′E. long. "From the date on which it was found," as Witherby remarks, "we may assume that this bird was in its winter quarters and was not on the way still farther south. It does not, therefore, give us a definite indication of the route by which some British-bred Swallows reach South Africa."

Migration of Swallows from Great Britain to South Africa is thus clearly established, and it is also certain that the birds commonly return to the same summer quarters, often with great exactness, in subsequent years. Much still remains to be learnt, and some of this the marking method may give in time. What route is followed between Great Britain and South Africa, for example; and are the identical winter quarters repeatedly sought out in the same way as the breeding places? Further, how do the migrations of British Swallows compare with those of Swallows native to other countries: can one, for instance, confirm the suggestion that, as Hartert expresses it, "the most northerly dwellers migrate farthest south, while the breeding birds of the Atlas Mountains probably go only to the oases of the Sahara for the winter"? These questions strike at the very roots of some of the great problems of migration.

The White Stork (*Ciconia ciconia*)

This species is taken as a second example of a summer visitor to Europe which is altogether absent from the area in winter, but the treatment of it will be for the most part confined to a brief summary of the results of study by the marking method. To these results this country has naturally been unable to contribute, but on the Continent Storks have been marked on a large scale and the results are of quite outstanding interest. These results have been published by Mortensen as regards Denmark, by Thienemann (and a few by Krüss) as regards Germany, and by Schenk as regards Hungary, and here an attempt will be made to combine them in a single statement.

The White Stork is only a wanderer, chiefly in spring, to the British Isles, and in France it breeds only in the north-east. Otherwise it is found in summer throughout the greater part of Europe, from southern Sweden southwards; in north-western Africa as far as the Gold Coast; and in

MIGRATIONS OF MARKED SWALLOWS.

Mainly after Witherby, adapted.

Showing localities of recovery of Swallows (*Hirundo rustica*) marked, mainly in Great Britain, as nestlings or as adults caught in the breeding-season. Records from the region of marking, which include many of birds returning in subsequent years to the places or regions of their birth or previous nesting, are omitted. Those shown refer to the seasons of passage or to sojourn in winter-quarters.

● Recoveries of Swallows marked in Great Britain.

✚ Recoveries of Swallows marked in Holland (Tangier recovery) and in Schleswig-Holstein, northern Germany (Lake of Constance recovery).

Asia Minor, Palestine, and other parts of western Asia. Farther east it is replaced by an allied race. In the time of year which is winter in the Northern Hemisphere it is found in Central and Southern Africa, and also in India southwards to Ceylon: the species is not known to breed in these southern regions.

The White Stork arrives in Hungary after the middle of March, the movement lasting until the end of April. According to Schenk (1909), arrival takes place earliest in the east and latest on the Adriatic coast, the difference in time being greater between east and west than between north and south. This indicates immigration from the south-east. In Alsace-Lorraine and in Switzerland, as Bretscher also shows, arrival is on an average about a month earlier than in Hungary, and the first date is sometimes in January, thus indicating arrival from a different direction: farther north, in Brunswick, the time of arrival is a little later than in Hungary. For localities in southern Sweden, Rendahl gives the time of arrival as being from 7th April to 1st May, becoming progressively later north-eastwards. From the maps accompanying a paper in Russian by Kaigorodov, it would appear that immigration into western Russia is from the south-west: the isochronal lines, of which the first is for 26th March and the last for 7th April, run north-west and south-east between the Baltic and Black Seas.

Departure from Europe takes place in August and the first half of September. Haagner states that the species is found in South Africa from the end of September to the end of April, but that a few birds also remain through the southern winter.

The birds which have been studied by the marking method, chiefly by the ringing of young birds in the nest, are those native to Denmark, to parts of Germany, and to Hungary: a few have also been marked in Holland and the Baltic States with German rings.

These recovery records of marked birds may conveniently be dealt with here in four main groups according to the portions of the migration tract to which they refer. There are in the first place records indicating a south-easterly autumn migration in Europe, and by way of the Mediterranean countries of Asia to Egypt. In the second place there are records indicating an alternative south-westerly route through Europe towards north-west Africa. Thirdly, there are records relating to passage through and sojourn in the African continent. Under each of these headings

such records as there are for the corresponding return movements in spring may also be considered. Finally, there are the records of recovery in the native areas in subsequent summers.

South-easterly autumn migration of White Storks in Europe and the Mediterranean countries of Asia, and the corresponding return passage in spring

Danish birds have been recovered in the autumn of the year of marking in northern Germany, Silesia, Galicia, northern Hungary and south-eastern Hungary. Some have also been recovered in subsequent autumns along the same path.

German birds have been recovered in autumn, especially in the year of marking, in Silesia, Poland, Galicia, Bohemia, Moravia and various parts of Hungary. Hungarian birds have been recovered in autumn in the Balkan States, and one has been recorded from Turkey in spring.

Except for one Hungarian bird recovered in Asia Minor in October of its second year, there is a curious, and possibly significant, absence of records for autumn passage through the Mediterranean countries of Asia, although for the return movement in spring and for the summer there are several records for the region : in Syria and Palestine two Danish, three Hungarian and four German birds have been recovered, and in Asia Minor one Danish bird and three Hungarian birds. It is to be remarked that in Europe the spring movement has provided the fewer records : these include some indicating the north-westerly return movement through Europe.

South-westerly autumn migration in Europe

The existence of this alternative direction of travel was first indicated by a record of a bird marked near Cassel, west-central Germany, and recovered in September of the same year near Barcelona, north-eastern Spain. (Lucanus, however, quotes from Homeyer a similar record dating from an early isolated attempt at marking in 1880.) Since then further records have been obtained through the marking of Storks in Baden, south-western Germany : of these one has been recovered in autumn near Barcelona, and five in autumn in southern France, one of them as far west as the Department of Basses-Pyrénées. It is possibly to this route also that one return movement record

should be assigned, namely, that of a Danish bird recovered in Algeria in June.

That there is also an intermediate north and south route by way of Italy is more faintly indicated. One German bird is believed to have been recovered in northern Italy, but the full details of the case could not be established. Another, marked (with an unofficial ring) in Bavaria, was recovered in the extreme south of Italy in its first autumn : but this case must be neglected because the bird had been taken from a nest in Styria and kept in semi-captivity in Bavaria (Schenk, 1909*c*.).

The existence of the south-westerly migration, almost at right angles to the apparently more usual south-easterly path, is of great interest. It also provides an opportunity of investigating a further question of much theoretical importance, namely, as to whether any distinct line can be drawn between the native areas of birds which follow these two very different lines of flight. In the meantime it would seem that such a line as this could be drawn from somewhere on the southern frontier of Germany northwards, and then north-westwards : but the data are still insufficient for any definite conclusion, and it may be that there is an area from which some birds emigrate in one direction and some in the other. It can at least be said that the south-easterly path is the usual one for birds native to northern and eastern Germany and to Denmark as well as undoubtedly for those native to Hungary ; and that it is the only one known to be taken by birds from north-western Germany and north-eastern Holland, although this latter statement rests only on a few records. With the possible exception of the Danish bird recovered in Algeria on return passage, the south-westerly route is known only in respect of birds marked in south-western Germany, and as regards one bird marked at Cassel in west-central Germany. Cassel lies not far to the west of places from which birds have taken the south-easterly path. Further marking in all the western regions of Germany and in Holland is required to decide the point.

Possible migration of White Storks towards the Indian Region

One record stands rather by itself, namely, that of a Hungarian bird recovered in October of its first year at Muscat, Oman, south-eastern Arabia. The direction certainly suggests winter quarters in India, but it may refer to a

EUROPEAN MIGRATIONS OF MARKED WHITE STORKS.

From the data of Mortensen, Thienemann and Schenk.

Showing the recovery localities in Europe and part of Asia of White Storks (*Ciconia ciconia*) marked as nestlings in Denmark, Germany (one in Holland), and Hungary (pre-war extent). Records from short distances in the first autumn, and all subsequent records from the region of origin, are omitted.

The recoveries are distinguished according to the origin of the birds, as follows :—

● Danish. ✚ German. ▲ Hungarian.

In the case of records for the first autumn a line connects the recovery locality to the marking locality.

stray bird or to a circuitous route to East Africa. It is certainly improbable that many birds native to the regions in which marking has been practised visit India, for the chances of recoveries being recorded there seem relatively good as compared with remote parts of Africa which have yielded not a few results.

(In this regard Schenk (1921) has brought to light three ancient records of marked Storks which are believed to have journeyed from Europe to India. In two of these cases, dating from 1813 and 1884, the marked bird is supposed to have brought back a note of its capture and release in India : in the third case details are not given. This kind of evidence, however, is best neglected.)

Migration and sojourn of White Storks in Africa

The most northerly African records for the autumn migration are those of a Danish bird in northern Abyssinia, and of German birds at Roseires, Sudan, and from the region just east of Lake Chad in Central Africa. All these refer to October of the year of marking. The next are of German birds recovered respectively on an island in Lake Victoria Nyanza in November of its first year, and in the Azande country near the Mbomu River, south-east of Lake Chad, in September of its second year. There follows an " autumn" record from what is now the Tanganyika Territory (and a completely undated record from the same region).

From northern Rhodesia southwards records become numerous. As many as sixty refer to Rhodesia, the Transvaal, Orange Free State, Natal, Basutoland and Cape Province. Most are for the eastern part of South Africa, but there are single records from Bechuanaland, the Kalahari Desert, and south-west Africa—this last a Hungarian bird.

Most of these records from South Africa are for the period November-March of the first year of life, and especially for December and January. A few relate to subsequent years at the same season. There are also, however, not a few records of birds remaining in South Africa during the southern winter, and of these eight fall in the middle of the season, June and July. There are also two May records for the fifth and sixth years of life respectively. The total number of South African records after the first year or so of life is so small that the scarcity of records at this season in subsequent years is not necessarily significant : but it

remains possible that it is only immature birds which fail to make the return journey to Europe.

For the season of the return movements towards Europe there are scattered records from northern Rhodesia, the Nyasaland Protectorate, the Tanganyika Territory, Kenya, and the Nile Delta—three from this last region. The June record from Algeria has already been mentioned.

The absence or scarcity of records relating to great parts of Africa naturally calls for no remark, and it is indeed wonderful that any have been obtained in some of the central regions. For this reason one hesitates to conclude in any very definite way that the recovery records trace out a migration route following the course of the Nile and the chain of great lakes, although it seems probable that some birds follow this general direction. Two records from the Chad region of Central Africa lie to the west of this path: either the path is a very broad one or there are alternative routes. In this regard one has to remember the records of south-westerly migration in Europe and the record from Algeria, but what further path is followed, and what winter quarters are reached, by the birds to which these relate is quite uncertain. (The two Central African records refer to birds marked in northern and north-eastern Germany, which one would expect to have travelled south-eastwards through Europe.) The joining together of recovery localities on a map in order to delineate a migration route has no justification except where the records are numerous and where some faith can be placed in the negative evidence which the absence of records in other possible regions provides. In this respect it is to be feared that some writers have erred on the side of hasty conclusions which do not fully take into account the limitations of the method, and which overlook the possibly fallacious indications of negative evidence relating to regions in which the human chances of recoveries being recorded are very small.

It does not even seem too certain that the main region of winter quarters is the eastern portion of South Africa, despite the great preponderance of records. The few records from the largely uncivilised western regions should possibly be given much more than their numerical value. It is also possible that many European birds of this species do not penetrate so far south at all: witness, for instance, a February record of a German bird in Kenya.

Return of White Storks to their native area in Europe

All the marking schemes have yielded abundant evidence showing that the birds return to their native area : there are in all 107 records of White Storks recovered in Europe in summers subsequent to that of marking. The return to the native locality is frequently exact, and the following analysis shows that it is usually at least approximate. In 54 cases the recovery locality was within, and very often well within, fifty English miles of the place of marking ; in 22 further cases the distance was at the most just over two hundred miles ; in 23 cases, recorded at some distance, early or late in the season, the birds were probably on migration and the records are therefore not significant for the present purpose. This leaves two cases in which birds were recovered in midsummer 450–500 miles from the place of marking. A bird marked in Denmark was recovered in July in Courland, Baltic States, when two years old, and another marked in north-western Germany was recovered in June in north-eastern Germany at the same age : presumably neither of these birds was breeding, but in any event they are obviously to be regarded as exceptional cases.

An interesting fact about these records showing return to Europe appears to have escaped notice hitherto. If the 107 cases are grouped according to the ages of the birds, from the second to the twelfth summer, their incidence is as follows : 11, 17, 28, 16, 14, 6, 3, 6, 4, 1, 1. The increasing figures in the first three years are all the more significant because it is very unusual to find such a thing in the statistics of marking results, the chances of records naturally diminishing as the surviving marked birds become fewer in the natural course : for the same reason the decrease after the first three years may be to some extent discounted. It can scarcely be doubted that the interpretation is that fewer birds return to the summer area at the ages of one and two years than subsequently : with this may be taken the evidence already given, relating almost entirely to immature birds, that some remain in South Africa and in intermediate regions during what is the breeding season in Europe. It may be added that the earliest definite record of the breeding of a marked Stork is for the age of five years (Thienemann, 1913*a*).

MIGRATIONS OF MARKED WHITE STORKS TO AFRICA.

From the data of Mortensen, Thienemann and Schenk.

Showing the recovery localities in Africa, Asia and parts of Europe, of White Storks (*Ciconia ciconia*) marked as nestlings in Denmark, Germany (one in Latvia) and Hungary. One Hungarian record from south-eastern Arabia is off the map: a Hungarian record from East Africa and a German record from Bechuanaland are omitted owing to indefiniteness of locality.

Recoveries are distinguished according to the origin of the birds, as follows:—

● Danish. ✚ German. △ Hungarian.

Area of numerous records (12 Danish, 21 German, and 32 Hungarian), too close together to be shown separately.

Conclusions

(The following conclusions are based solely upon the exact evidence given by the marking records discussed, and ignore information from other sources.)

White Storks, native to Denmark, north-eastern Holland, northern and eastern Germany, and Hungary, migrate in autumn south-~~west~~wards towards the eastern Mediterranean and return by a corresponding north-westerly route in spring. Records for Asia Minor, Syria, Palestine, and Egypt nearly all refer to the spring passage, although what significance, if any, should be given to this fact seems uncertain.

White Storks, native to parts of western Germany, migrate south-westwards in autumn through France and Spain : the further extension of this route and its use on the return journey are not known, except in so far as one record of a Danish bird recovered in Algeria in June may be relevant. It remains to be determined whether the birds taking this and the previous course, respectively, inhabit distinct native areas, as the available evidence would appear to suggest.

So far as one may presume upon the negative evidence given by the absence of records from other regions, White Storks native to Denmark, Germany, and Hungary traverse the western and central regions of the African continent on their further migration and on the return journey. Large numbers of them " winter " (in the southern summer) in the eastern parts of South Africa : some at least reach the western parts and others possibly do not come so far south. One record of a Hungarian White Stork in south-eastern Arabia might be taken as an indication of a possible migration of European birds to the Indian region.

White Storks, bred in Denmark, Germany, and Hungary return to their native localities, commonly with some exactness, in subsequent summers, both as immature and as breeding birds. The exceptions do not seem important. Summer records from Africa and the Mediterranean countries of Asia show that some birds, possibly only when immature, do not always perform the full return journey, and may even remain in South Africa during the southern winter.

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SOURCES OF DATA SHOWN ON MAP.—The map of the migrations of marked Swallows is only slightly adapted, with the addition of more recent records, from a map originally published by Witherby (1922*d*) and based chiefly on his own records. Full particulars of the data have already been given above.

The two maps of the migrations of marked White Storks are based on a combination of the published data of Mortensen (1920), Thienemann (1903–24*a*) and Schenk (1908–24*b*), which have been summarised above; one German record published by Krüss (1918) is also included. Maps showing parts of the data have been published by Mortensen (1920), Thienemann (1910*c*, 1912*a*), and Schenk (1910*b*): these have frequently been reproduced by others or used as the basis of rough attempts at combined presentation.

CHAPTER XI

THE MIGRATIONS OF THE LAPWING

Comparison with preceding examples—Distribution—Movements observed in the British area—Method of dealing with and interpreting marking results—The results of the Aberdeen University inquiry—Conclusions drawn therefrom—Other British marking results—Foreign marking results—General conclusions.

THE species selected as examples in the preceding chapter were both migrants of the more obvious kind, birds which entirely vacate the greater part of their breeding areas in winter, and which perform long journeys extending beyond the Equator. This third example, on the other hand, is a species which is represented throughout the year in a large part of its range and of which some individuals are probably stationary : nevertheless, complicated movements on a great scale take place and in some cases the individual journeys are of considerable length.

The Lapwing (*Vanellus vanellus*) breeds in Northern and Central Europe and Asia, becoming scarce above about 60°N. lat. : in Europe it is found in summer in the south of Spain, but not in Greece and southern Italy ; and it also breeds sparingly in Morocco. In winter it becomes widespread in the Mediterranean basin, including the African side, and also reaches the Canaries and the Azores, Persia, northern India, Burma, China, and Japan. Casually the Lapwing occurs in Jan Mayen, Iceland, Greenland, Canada, Alaska, the Bahamas and the Barbadoes.

In the British Isles the Lapwing is found all the year round, but it does not breed in some parts of the south of England, and in winter it is absent from many inland districts. Different individuals are respectively residents, summer visitors, winter visitors, and birds of passage. The complicated movements have been worked out by Eagle Clarke in great detail, and of his conclusions some brief account may first be given.

" Flocking " takes place at the close of the nesting season, and in July or even late June slight movements of a more or

less erratic nature may be observed. In August the birds begin to leave the more northerly parts of the country, and it may be noted that in the northern isles there is an interval between the departure of the last summer visitors and the arrival of the first overseas immigrants. In September the southward movement within the British Isles is in full swing; in October it reaches its height, but it persists still in mid-November. By October the higher inland districts are practically deserted for the winter. The movements include an immigration to Ireland from Scotland in October and November.

Autumn immigration from north-western Europe takes place from early October to mid-November. It affects the east coast of Scotland from Shetland southwards, and the northern section of the east coast of England, but movements affecting a great stretch of coast-line simultaneously do not usually occur. The total number of immigrants is not very great, for the species is by no means abundant in north-western Europe.

In October and early November an immigration from the east (and south-east) takes place on the coast between the Thames and the Wash and the Humber. There is no evidence of immediate southward emigration of immigrants from either source: most of the birds certainly remain within our area for some time, although many must eventually cross the Channel.

There is no evidence of any cross-Channel emigration in September or October, although the existence of slight movements of this nature is not improbable. Considerable emigration takes place in November, the movements being associated with general movements down the east and west coasts of England.

There are also notable winter movements subsequent to the ordinary migration season. These movements are, indeed, of a far more general and striking character than the autumnal migrations, but their extent and the time of their occurrence depend entirely on the severity of the season. In seasons when no very severe weather has occurred until late in the winter, there may be cross-Channel emigration in the middle of February, and southward movement within the British Isles as late as mid-March. In severe winters the weather movements in west-central Europe also give rise to an immigration on the southern section of the east coast of England, the birds afterwards spreading westwards across the country.

Some birds return to their island haunts at the end of January or in February, but very often have to beat a temporary retreat. The normal time for returning to summer quarters is between the end of February and the middle of March, except in very late seasons. These movements include a return journey from the north-east of Ireland to the west of Scotland. There is also a south-easterly emigration from Wexford at the end of February: the autumn counterpart of this movement has not yet been recorded, and it is also uncertain whether the birds which participate are native to England or to the Continent.

Spring immigration from Southern Europe is a very inconspicuous movement, occurring in the latter half of March. From late February to early April, however, Lapwings are recorded crossing from the south of England in a north-westerly direction to the south-east of Ireland, although no corresponding south-easterly migration has been noted in autumn. It will be noted that Lapwings thus cross the Irish Channel at the end of February in two opposing directions.

Passage and emigration to north-western Europe begin at the end of February or the beginning of March, and last until the middle of April, after which only stragglers are noted on migration. The movements affect both coasts of Great Britain and also the northern isles: some overland crossing also takes place. Emigration to the east, a counterpart of the autumn movement from that quarter, doubtless exists, but it has not yet been recorded.

The special purpose of this chapter, however, is to give an account of the results of the marking method as applied to the Lapwing, more particularly in the British area. The species has been studied by this means under both the Aberdeen University and *British Birds* inquiries. Of these the second is still in active progress, and the results to date are not yet completely available in collected form. It is accordingly proposed to deal fully with the Aberdeen University records by themselves in the first instance and to make briefer subsequent reference to the other British data, and to the foreign data which have been published.

It is also proposed to give the analysis of the Aberdeen data in extensive form by way of an example of the methods employed by the writer in analysing and interpreting the results of bird-marking in general. These methods have been applied to several of the other examples dealt with in these chapters, but in the other cases the account given will

be abbreviated to show only the results of analysis which are considered significant, no attempt being made, as in this instance, to show the whole of the data and the method of working out.

The method adopted has been based on a system of grouping in accordance with the districts in which the birds were marked. A distinction has also been maintained between birds marked when young and birds obtained under other circumstances, the latter class being further subdivided under seasonal headings. The object in view has been to keep together records relating to birds originally belonging to presumably homogeneous groups, and in this way to eliminate errors due to possible geographical differences. But where the grouping has revealed no obvious divergency, the separate treatment of the groups is abandoned.

The data thus grouped have been analysed, as a rule, in three different ways. The principal analysis is a seasonal one, the recovery records of all birds of a particular group, or series of similar groups, being classified according to locality and calendar month. In this main analysis the records of birds recovered in their first, second, or subsequent seasons, are treated alike : to exclude the possibility of error from this source a second analysis is added in which the classification is by localities and ages. The third analysis is similar to the second, but is based on the calendar year (reckoned from summer to summer) instead of on the year of the bird's life, and it thus affords a check on possible errors due to meteorological differences between one winter and another.

For the purpose of grouping the data now under consideration the following arbitrary districts were defined :

North of Scotland : From Inverness-shire, Nairn, and Moray (inclusive) northwards.

North-east of Scotland : Aberdeenshire, Banffshire, and Kincardineshire.

Central Scotland : The remainder, as far south as the Firths of Forth and Clyde.

South-east of Scotland : Eastern side, south of the Firth of Forth.

South-west of Scotland : Western side, south of the Firth of Clyde.

North of England : From Yorkshire and Lancashire (inclusive) northwards.

South of England : The rest of England and Wales, but, in effect, almost entirely the southern counties.
Ireland.

The following table gives the numbers of Lapwings marked during the course of the Aberdeen University inquiry, and the numbers recovered in the respective categories.

TABLE A

NUMBERS OF LAPWINGS MARKED AND RECOVERED

Seasons of marking as chicks	Numbers marked (by regions)								Total	Numbers recovered (by seasons of marking)
	N. Scotland	N.E. Scotland	C. Scotland	S.E. Scotland	S.W. Scotland	N. England	S. England	Ireland		
1909	–	24	1	–	–	–	–	–	25	1
1910	17	232	23	2	25	–	–	–	299	10
1911	14	379	11	7	1	8	26	–	446	6
1912	43	386	38	12	15	88	29	3	614	14
1913	157	335	58	29	10	25	1	8	623	19
1914	48	395	46	16	3	11	–	31	550	9
1915	–	210	–	5	12	12	–	–	239	2
1916	–	114	71	27	13	3	7	–	235	1
1917	–	65	–	1	17	–	–	–	83	2
1918	–	8	–	–	–	–	–	–	8	–
1919	–	9	–	–	4	–	–	–	13	–
Not as chicks.	–	4	1	1	–	1	–	–	7	–
Total .	279	2161	249	100	100	148	63	42	3142	64
Numbers recovered (by regions of marking).	3	43	7	–	6	3	2	–	64	2.0%

The percentage of marked Lapwings recovered is thus approximately 2·0, if calculated on the total. But when calculated for separate years the figures vary from 0·4 to 3·3 per cent if all years in which over 200 were marked be taken, and from 1·3 to 3·0 per cent if limited to those years in which over 400 were marked. Similarly, the percentage varies from 1·0 to 2·8 when calculated separately in the case of the single region in which the number was much larger. In making comparisons between the numbers of records falling under particular headings, therefore, it would be unsafe to attach significance to any figure which

could not be assumed to represent a total of several hundred marked birds. Numerical contrasts are accordingly permissible only between the widest categories, and analysis must be for the most part qualitative rather than quantitative.

Table B gives a complete list of all the recoveries, of Lapwings marked with Aberdeen University rings, grouped in the manner already explained.

TABLE B

LIST OF RECOVERIES OF MARKED LAPWINGS

Season of Marking	A.U. No.	Date of Recovery	Place of Recovery
		Marked as Chicks in the North of Scotland.	
1912	27388	20.8.14	Place of marking.
1913	35086	ca. 22.11.13	Co. Westmeath, Ireland.
	32369	early 1.14	nr. Oporto, Portugal.
		Marked as Chicks in the North-East of Scotland.	
1909	32	13.6.09	Place of marking.
1910	13487	15.7.10	Place of marking.
	13273	6.8.10	Place of marking.
	14077	? Oct. (possibly Nov.)10	nr. Oporto, Portugal.
	12730	ca. 19.11.10	Co. Tipperary, Ireland.
	8545	ca. 22.11.10	Co. Roscommon, Ireland.
	12731	29.12.10	nr. Elvas, Alemtejo, Portugal.
	14370	ca. 5.2.11	Co. Cork, Ireland.
	14699	13.2.11	Co. Limerick, Ireland.
	12214	ca. 1.1.12	Co. Roscommon, Ireland.
1911	20074	17.10.11	Queen's Co., Ireland.
	16828	7.11.11	Area of marking.
	12302	20.8.13	Place of marking.
	17950	3.7.15	Place of marking.
	15319	20.2.17	Co. Wicklow, Ireland.
1912	27027	2.1.13	Anglesey, Wales.
	30595	ca. 10.1.13	nr. Guarda, Portugal.
	30302	27.8.13	Place of marking.
	15005	24.2.15	Cardigan, Wales.
	30301	8.12.15	Place of marking.
	28461	ca. 6.2.17	Devon, England.
	27439	late 1.24	Co. Galway, Ireland.

Season of marking	A.U. No.	Date of Recovery	Place of Recovery
1913	28091	15.8.13	Place of marking.
	32592	20.8.13	Place of marking.
	21935	ca. 24.1.14	Co. Mayo, Ireland.
	23195	ca. 29.1.14	Landes, France.
	21491	ca. 5.2.14	Co. Tipperary, Ireland.
	34455	ca. 8.2.14	Co. Galway, Ireland.
	30553	ca. 20.11.14	Co. Limerick, Ireland.
	22877	19.2.15	Co. Roscommon, Ireland.
	36420	13.1.16	Place of marking.
	32583	29.11.18	Place of marking.
1914	38142	early 9.14	Place of marking.
	38322	23.12.14	Co. Wicklow, Ireland.
	37680	24.12.14	Co. Down, Ireland.
	37672	13.12.15	Co. Clare, Ireland.
	34921	23.2.16	Area of marking (a few miles beyond boundary).
	38390	13.3.16	Co. Durham, Ireland.
	38342	early 1.17	Co. Cork, Ireland.
	38112	8.2.17	Co. Tipperary, Ireland.
	34424	16.1.20	Co. Durham, England.
1915	34213	24.11.16	nr. Oporto, Portugal.
	34210	16.12.17	nr. Oporto, Portugal.
	Marked as Chicks in Central Scotland.		
1910	13398	30.12.11	Co. Westmeath, Ireland.
1912	24224	ca. 20.1.13	Co. Mayo, Ireland.
	21726	23.10.14	Queen's Co., Ireland.
	27964	6.2.17	Co. Sligo, Ireland.
1913	32116	ca. 2.1.14	Co. Leitrim, Ireland.
	21775	early 1.14	nr. Oviedo, Northern Spain.
1914	29946	2.16	N. Cornwall, England.
	Marked as Chicks in the South-west of Scotland.		
1912	25240	11.1.13	Queen's Co., Ireland.
1913	32395	early 1.14	nr. Oporto, Portugal.
	32396	9.1.14	nr. Oporto, Portugal.
1916	40754	9.12.19	Co. Londonderry, Ireland.
1917	41305	ca. 10.12.17	Co. Londonderry, Ireland.
	41304	ca. 21.10.18	Co. Sligo, Ireland.

Season of marking	A.U. No.	Date of Recovery	Place of Recovery
		Marked as Chicks in the North of England.	
1911	13192	ca. 15.12.12	Co. Kildare, Ireland.
1912	28065	2.12.12	Co. Kilkenny, Ireland.
1913	22191	ca. 18.1.14	Landes, France.
		Marked as Chicks in the South of England.	
1912	22393	19.2.13	nr. place of marking.
1913	36340	ca. 8.5.20	nr. place of marking.

As the records from the various regions appear to be similar in character, the Scottish and north of England birds are treated as a single group for purposes of further analysis, the two south of England cases being neglected. Table C gives the analysis according to the months in which the reappearances were recorded.

TABLE C

SEASONAL ANALYSIS OF RECOVERIES OF LAPWINGS MARKED AS CHICKS IN SCOTLAND OR THE NORTH OF ENGLAND

Month	Area of Marking	*North of England	*Wales	*Devon and Cornwall	Ireland	S.W. France	N. Spain	Portugal	Total
May	–	–	–	–	–	–	–	–	–
June	1	–	–	–	–	–	–	–	1
July	2	–	–	–	–	–	–	–	2
August	6	–	–	–	–	–	–	–	6
September	1	–	–	–	–	–	–	–	1
October	–	–	–	–	3	–	–	1	4
November	2	–	–	–	4	–	–	1	7
December	1	–	–	–	8	–	–	2	11
January	1	1	1	–	7	2	1	4	17
February	1	–	1	2	8	–	–	–	12
March	–	1	–	–	–	–	–	–	1
April	–	–	–	–	–	–	–	–	–
Totals	15	2	2	2	30	2	1	8	62

* All records under these headings relate to birds marked in north-east or Central Scotland.

The above table reveals the following facts:

(*a*) A few birds are recorded in their native areas throughout the winter: considering the favourable conditions for records, the proportion remaining is probably a small one.

(*b*) Greater numbers are recorded from Ireland from October to February, representing about 50 per cent of the whole list of records.

(*c*) Some are recorded from Portugal from October to January: considering the presumably unfavourable conditions for records, the proportion of birds these cases represent is probably a large one.

(*d*) A few birds are recorded from northern Spain, south-western France, and parts of Great Britain south of the localities of marking, but only, it so happens, in January and February. (The absence of autumn and early winter records from these regions might be taken as suggesting that the birds reaching Portugal do so by way of Ireland and a long sea-crossing, some perhaps returning by a coastal route, but there is no positive evidence on this point.)

(*e*) Despite the favourable conditions for records there is an entire absence of recoveries at places only a moderate distance from those at which the birds were marked, and there are only a very few from more distant parts of Great Britain. The birds would therefore appear to be either definitely stationary or definitely migratory, in the latter case performing comparatively quick journeys rather than gradual movements.

TABLE CC

SEASONAL ANALYSIS OF RECOVERIES IN IRELAND OF LAPWINGS MARKED AS CHICKS IN SCOTLAND OR THE NORTH OF ENGLAND

Month	North	East	West	South	Total for Ireland
October . .	—	2	1	—	3
November. .	—	1	1	2	4
December .	3	4	—	1	8
January . .	—	1	5	1	7
February . .	—	1	3	4	8
Total . .	3	9	10	8	30

The number of Irish recovery records justifies a supplementary analysis of these in more detail, and this is provided in Table CC. For this purpose Ireland is divided into four quarters—north, east, west, and south—which have for convenience been taken as identical with the four provinces —Ulster, Leinster, Connaught, and Munster—as they stood prior to the political changes which have occurred since the date of the investigation.

From this table it is evident that the records are evenly distributed among the three southern regions, but are few in number in the northern one. The only northern records, and the majority of those from the eastern region, refer to the first half of the winter season, while most of the records from the other two regions occur in the second half: this might be explained either by a local south-westerly movement during the winter or by longer journeys on the part of later arrivals from Great Britain, but the numbers, when thus subdivided, are rather small to be accepted as significant.

The following table analyses the same records as were dealt with in Table C, but does so in accordance with the ages of the birds at the time of recovery:

TABLE D

AGE ANALYSIS OF RECOVERIES OF LAPWINGS MARKED AS CHICKS IN SCOTLAND OR THE NORTH OF ENGLAND

Year of the Bird's Life	Area of marking		*England and Wales	Ireland	S.W. France and N. Spain	Portugal	Total
	June-Sept.	Oct.-Feb.					
First year	6	1	1	16	3	6	33
Second year	1	1	2	7	–	1	12
Third year	2	1	1	3	–	1	8
Fourth year	–	1	–	1	–	–	2
Fifth year	1	–	1	1	–	–	3
Sixth year	–	1	1	1	–	–	3
Twelfth year	–	–	–	1	–	–	1

* See footnote to Table C.

The decreasing number of records in successive years naturally follows, of course, from the decreased total of survivors, but it may also represent a lower mortality rate after the first season. The records for the first three

seasons suffice to show that age is an unimportant factor in determining the character of the movements performed.

The following table is similar to the foregoing, but is based on calendar years :

TABLE E

ANNUAL ANALYSIS OF RECOVERIES OF LAPWINGS MARKED AS CHICKS IN SCOTLAND AND THE NORTH OF ENGLAND

Year of Recovery	Area of marking		*England and Wales	Ireland	S.W. France and N. Spain	Portugal	Total
	June-Sept.	Oct.-Feb.					
1909–10	1	–	–	–	–	–	1
1910–11	2	–	–	4	–	2	8
1911–12	–	1	–	3	–	–	4
1912–13	–	–	1	4	–	1	6
1913–14	4	–	–	5	3	3	15
1914–15	2	–	1	5	–	–	8
1915–16	1	3	2	1	–	–	7
1916–17	–	–	1	4	–	1	6
1917–18	–	–	–	1	–	1	2
1918–19	–	1	–	1	–	–	2
1919–20	–	–	1	1	–	–	2
1923–24	–	–	–	1	–	–	1

* See footnote to Table C.

The above table has been retained mainly as an example of the method employed, for, as has already been pointed out, excessive subdivision of the available total renders the separate items too small to be regarded as quantitatively significant.

Other British records

Witherby's results for this species have not yet been fully published in collected form, but they now consist of a still larger series of records than that which has just been dealt with : for present purposes a brief review of them will suffice. Most of these records also refer to birds native to the region defined above as " Scotland and the North of England," and several more to the contiguous county of Cheshire. Without attempting any analysis of these records, it may be said that they appear to be closely similar in nature to those of the other inquiry. There are also some records of birds native to the south of England. These appear to differ chiefly in showing no migration to Ireland : they

include records from France, Spain, and Portugal, and one of special interest, from Morocco (B.B. 13,961 : Warwickshire, 22.6.11 ; near Casablanca, 7.1.14).

Birds marked abroad and recovered in the British Isles

The following records all refer to Lapwings marked on the Continent in summer and recovered in England, principally in the south-east, in winter:

TABLE F

Ring No.	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
Rossitten 18,039	10.6.13	Isle of Fehmarn (Baltic), Germany.	11.2.15	Hickling, Norfolk.
Rossitten 17,625	29.5.13	Domnau, East Prussia	25.2.16	Chichester, Sussex.
Rossitten 18,302	2.6.13	nr. Hapsal, Esthonia.	11.11.13	nr. Louth, Lincolnshire.
Leiden 3,330	15.6.13	Egmond, North Holland.	25.12.13	Knowle, Warwickshire.
Fr.-Sund, 47	15.5.21	nr. Frederikssund, Denmark.	13.10.21	Colchester, Essex.
Fr.-Sund, 40,041	23.5.23	Sjaeland, Denmark.	15.11.23	Staffordshire.
Leiden 20,812	15.6.20	Vogelenzang, Holland	13.11.20	Stallingborough, Lincolnshire.
Leiden 25,630	29.6.19	Lisse, Holland.	13.12.20	Guernsey, Channel Islands.
Göteborg 2,302 c	–.6.24	Öland, Sweden.	–.1.25	nr. Louth, Lincolnshire.

Other foreign records

According to Van Oort, Lapwings marked in Holland have also been recovered in France (chiefly the north and west), in Spain (north-west and south-west), in Morocco (one), and (as quoted by Tait) in Portugal.

A Lapwing marked (with a Heligoland ring) as a chick in the Baltic coastal region of northern Germany has, according to Weigold, been recovered in Holland on the south-eastern shore of the Zuider Sea. Others marked (with Rossitten rings) as chicks in the same region, as recorded by Thienemann, have been recovered in winter in Holland, in western and south-western France, and in western and southern Spain. Thienemann has also a record of a Lapwing marked as a chick near Breslau, south-eastern Germany, and recovered in winter near Milan, northern Italy.

Schenk records the recovery of Lapwings marked in Hungary either as chicks or as adult breeding birds. Some

MIGRATIONS OF MARKED LAPWINGS.

From published data from all sources.

Showing the recovery localities of Lapwings (*Vanellus vanellus*) marked in various parts of Europe, mainly as young birds, but in a few cases as adults caught in the nesting season. Records from the region of marking are omitted.

- Recoveries in the rest of the British Isles of Lapwings marked in Scotland and northern England (Cheshire and Yorkshire northwards).
- Recoveries abroad of Lapwings marked in Great Britain.

Other recoveries are distinguished, according to the origin of the birds, as follows :—

Dutch. Danish. Swedish. North German.
Esthonian. Silesian. Hungarian.

of these have been recovered in winter in Italy, especially in the north, in southern France, in eastern Spain, and in Algeria. A bird marked in Hungary in winter was also recovered near Marseilles, southern France, rather more than three years later.

Conclusions

The following general conclusions may be drawn from the results of the marking method so far obtained :

(1) A few Lapwings native to different parts of Great Britain remain in their native districts during the winter.

(2) Many Lapwings native to Scotland and the north of England are to be found in Ireland in winter, the records from that country being fewest in its northern portion : Lapwings native to the south of England have not been shown to visit Ireland.

(3) Many Lapwings native to different parts of Great Britain are to be found in Portugal in winter. Northern Spain and south-western France are also known to be visited in the later winter months, possibly on return passage. One record, of a bird marked in Warwickshire, indicates that the movement extends in some degree to Morocco.

(4) A few Lapwings native to Scotland visit the north of England, Wales, and the extreme south-west of England in the later winter months, possibly on return passage from the south.

(5) Lapwings native to Great Britain would appear to be either definitely stationary (in a few cases) or definitely migratory, few being recorded at moderate distances from the places of marking.

(6) Holland, Denmark, southern Sweden, northern Germany, and Esthonia are among the regions from which come Lapwings visiting the south-eastern area of England in winter.

(7) Migration of Lapwings has also been demonstrated from Holland to France, Spain, Portugal, and Morocco ; from northern Germany to Holland, western and south-western France, and western and southern Spain ; from south-eastern Germany to northern Italy ; and from Hungary to Italy, southern France, eastern Spain, and Algeria.

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For references to the sources of single foreign records see end of Chapter XV.

SOURCES OF DATA SHOWN ON MAP.—The map of the migrations of marked Lapwings is based, as regards birds of British origin, on the present writer's own data, given fully above, and on the data published by Witherby (1910–25*c*). Particulars of the records of birds of Continental origin, with reference to the sources of the data, have been given above.

CHAPTER XII

THE MIGRATIONS OF THE STARLING

Distribution—Movements observed in the British area—Results of the marking method—Summary and discussion of marking results—Conclusions drawn from the marking method.

THIS next example resembles the preceding one in the matter of its status as a migrant, being a species which is represented throughout the year in all but the extreme northern and extreme southern portions of its total range and of which some individuals are wholly stationary, but which is nevertheless subject to complicated migration movements on a large scale. The Starling (*Sturnus vulgaris*) is found as a breeding species throughout Europe, except in Spain, Portugal, and southern Italy, and over a great part of western Asia. In winter it is absent from the more northern portions of this range, and at that season its distribution is extended southwards to include such regions as Spain and northern Africa. The British Isles lie within the zone in which the species is represented throughout the year, although many of the individuals are migratory, but it may be remarked that it is only of recent years that the Starling has become a regular inhabitant of many parts of Scotland, northern England, and Ireland.

Movements observed in the British area

The British movements of the Starling have been worked out by Eagle Clarke from the data collected at light-stations for the British Association Committee, and this information has more recently been supplemented by the reports of the Migration Committee of the British Ornithologists' Club. As early as June young Starlings of the year may be seen in flocks, and local movements of these take place ; later on, both old and young tend to move towards the southern and western districts of the British Isles. In autumn there is also a large immigration from the Continent, partly from Central Europe along an east-to-west route which strikes the southern half of the east coast of England, and partly

from Northern Europe by a south-westerly route which strikes the eastern seaboard of Great Britain along the whole of its extent except the southernmost portion: south of the Humber the two movements overlap. The immigration from Central Europe takes place, mainly by day, from about the last week in September until early in November, while the more northerly movement is largely nocturnal and slightly later both in beginning and in ending. From the end of July onwards there is an emigration from the southern coasts of the British Isles to winter quarters in Southern Europe. The earlier emigrants are thought to be native birds which are summer visitors to this country, while the later ones are probably in large part birds of passage which have arrived with the winter visitors from Central and Northern Europe. Any or all of these different autumn movements may be repeated and extended during spells of severe weather in the winter.

The spring movements are counterparts of those observed in autumn. The immigration from the south takes place from the latter part of February until early April, and the return of winter visitors and birds of passage to Central Europe from the middle of February to the end of March, and to Northern Europe from the middle of March to the end of April.

Results of the marking method

The study of mass movements upon which the foregoing summary is based has recently been supplemented and extended by the records of the recovery of marked birds, and of these it is now proposed to give some account. The data to be summarised are those which have been obtained by Witherby up to the time of completing the list published in the magazine in December, 1925, and those which were obtained by the present writer (1921) during the Aberdeen University Inquiry. The numbers of marked birds to be dealt with are as follows:

	Total marked to 31st Dec. 1924	Total Recovered	Percentage Recovered
British Birds . . .	9,526	474	5·0
Aberdeen University .	1,900	62	3·3
	11,426	536	4·7

The recovery figures for the Aberdeen Inquiry may be regarded as final, whereas those for the *British Birds*

scheme are only partial, seeing that many of the more recently marked birds are still likely to be recorded. As regards the difference in percentage between the two sets of records it should be remarked that the number of recoveries is to some extent artificial, a very large number of records being due to the retrapping activities of some of the markers. If all records from the places of marking and from within very short distances be excluded, the recovery rates for the two inquiries work out at an almost identical figure of approximately 0·5 per cent.

All the recovery records relate to birds marked in Great Britain. Among the *British Birds* records English-marked birds predominate, and among the Aberdeen records Scottish-marked birds are in the majority. Taking the two sets together, various sub-analyses have been made on a territorial basis without revealing any significant differences, and it would accordingly seem that the whole series can be treated as a single geographical group.

Locality within Great Britain being thus left out of account, the records may be conveniently grouped in the following divisions according to the season and circumstances of marking :

(A) Birds marked as nestlings : obviously native to the places of marking.

(B) Birds (all or mainly adults) caught and marked in summer (April–September, but principally in the breeding season) : presumably native to the places of marking.

(C) Immature birds caught and marked in the late summer, possibly at a distance from their birth-places in view of the early movements which young birds are known to make. (This category includes only the birds specifically described by the markers as immature : a few others may thus be included in the previous group.)

(D) Birds caught and marked in winter (October–March), except those marked at lighthouses : the relation of place of marking to native locality is unknown, but these are probably a mixture of stationary birds and of winter visitors from other districts or from abroad.

(E) Birds caught and marked at lighthouses while on migration.

TABLE A

ANALYSIS OF RECOVERY RECORDS OF STARLINGS MARKED AS NESTLINGS IN GREAT BRITAIN

Year of Bird's Life (dating from 1st April of summer of marking)	Recovered at or near place of marking		Recovered at a distance	
	April-September	October-March	April-September	October-March
First year . .	20	23	5	5
Second year . .	15†	17*	1	—
Third year . .	12	7†‡	—	1
Fourth year . .	3	3‡	—	2*
Seventh year . .	1	—	—	—
Total . .	51‖	50§	6	8

Grand Total: 115 records, representing 112 individuals.

* † ‡ Three birds reported twice each, once in each category indicated.

‖ Six (two in each of the second, third and fourth years) reported as nesting.

§ Monthly incidence: October 6, November 12, December 5, January 7, February 10, March 9.

TABLE AA

(*Details of cases in Table A, columns* 4 *and* 5)

PARTICULARS OF STARLINGS MARKED AS NESTLINGS AND RECOVERED AT A DISTANCE

Ring No.	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
B.B. 49706	10.5.14	Berkshire.	28.6.14	Buckinghamshire.
B.B. 84466	20.5.15	Shropshire.	–.7.15	Worcestershire.
B.B. 81886	28.5.15	Staffordshire.	18.7.15	Montgomeryshire.
B.B. 42667	29.5.13	Staffordshire.	13.8.13	Cheshire.
B.B. 96245	23.5.20	Staffordshire.	–.8.20	Lincolnshire.
A.U. 36353	19.5.13	Hampshire.	17.1.14	Cornwall.
B.B. 10899	31.5.11	Stirlingshire.	ca. 20.1.12	Co. Donegal, Ireland.
B.B. 42678	29.5.13	Staffordshire.	13.2.14	Lancashire.
B.B. 91567	22.5.18	Stirlingshire.	13.9.19	Cheshire.
B.B. 87755	2.6.16	Staffordshire.	–.3.19	Derbyshire.
B.B. 19056	24.5.13	Staffordshire.	29.1.17	Co. Roscommon, Ireland.
B.B. 41085	20.6.13	Berkshire.	8.2.15	Place of marking (released with new ring, 83837).
			–.2.17	Cornwall.
B.B. 54309	30.5.22	Westmorland	–.11.22	Co. Durham.
B.B. 58116	10.6.23	Westmorland	–.10.23	Co. Fermanagh, Ireland.

The series of tables (similarly lettered) given here presents analyses of the recovery records of birds falling into these five marking groups. A supplementary table (F) gives particulars of Starlings marked abroad and recovered in the British Isles.

From Tables A and AA it is apparent that many of the birds are stationary, numbers being recorded from the same place or district throughout the year (distances of

TABLE B

ANALYSIS OF RECOVERY RECORDS OF STARLINGS CAUGHT AND MARKED AS ADULT BIRDS IN GREAT BRITAIN IN SUMMER (APRIL–SEPTEMBER)

(*A few full-grown immature birds may have been included by the markers*)

Year of Bird's marked Life (dating from 1st April of summer of marking)	Recovered at or near place of marking		Recovered at a distance	
	April-September	October-March	April-September	October-Marc
First year . .	9	9	—	2
Second year . .	12*	4	—	—
Third year . .	1*	—	—	—
Fourth year . .	1*	1	—	—
Fifth year . .	—	—	—	—
Sixth year . .	—	1	—	—
Total . .	23†	15	—	2‡

Grand Total: 40 records, representing 38 individuals.

* One thrice, once in each of these categories.

† Five recorded as nesting.

‡ B.B. 11772 and 11774, both marked in Lincolnshire on 10.9.10, and recovered in December of the same year in Yorkshire and Pembrokeshire respectively.

less than twenty miles have been ignored). Of the records of birds recovered away in summer, four represent short early movements of young birds and the fifth is really an autumn record. Of the records of birds recovered away in winter, the most interesting are the three showing migration to Ireland—one from central Scotland, one from the north of England, and one from the English Midlands: the case of the Berkshire bird recovered in Cornwall in its fourth

winter after having been recorded at home in its second, may also be noted.

There is a further British record of special interest which should be mentioned under this heading. Among a small number of records obtained by Ticehurst, when using his own rings, is one of a Starling (Ticehurst 72) marked as a nestling at Tenterden, Kent, on 22nd May, 1908, and recovered at Berck Plage, near Boulogne, France, on 8th October, 1908. This appears to be the only case of an undoubted native Starling being recovered in France and,

TABLE C

ANALYSIS OF RECOVERY RECORDS OF STARLINGS CAUGHT AND MARKED AS IMMATURE BIRDS IN GREAT BRITAIN IN LATE SUMMER

(*Most of these birds were marked in Lincolnshire in July or August*, 1913)

Year of Bird's Life (dating from 1st April of summer of marking)	Recovered at or near place of marking		Recovered at a distance	
	April-September	October-March	April-September	October-March
First year . .	9	15	—	4
Second year . .	2	1	—	2
Third year . .	2	3	2	—
Fourth year . .	—	—	—	—
Fifth year . .	1	—	—	—
Total . .	14	19	2	6

Grand Total: 41 records and individuals.

moreover, it represents what is practically the minimum possible in the way of a cross-Channel journey.

The records given in Table B show that many of the birds are stationary, and there are only two cases of recovery at distances exceeding about twenty miles. Of the birds recovered at the place of marking, five (all in Kent, as it happens) were recorded as nesting—two later in the same summer, two in the second summer, and one in the second summer (first and second broods) and again in the third and fourth summer: this last bird, a female, was also nesting when originally marked and is therefore known to

TABLE CC

(Details of cases in Table C, columns 4 and 5)

PARTICULARS OF STARLINGS MARKED AS IMMATURE BIRDS AND RECOVERED AT A DISTANCE

Ring Number	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
B.B. 16812	11.9.12	Lincolnshire.	22.3.14	Cambridgeshire.
B.B. 46363	11.8.13	Lincolnshire.	1.11.13	Lancashire.
B.B. 46284	9.8.13	Lincolnshire.	2.12.13	Lancashire.
B.B. 46375	11.8.13	Lincolnshire.	2.12.13	Co. Kilkenny, Ireland.
B.B. 46322	9.8.13	Lincolnshire.	17.1.14	Nottinghamshire.
B.B. 46258	8.8.13	Lincolnshire.	30.10.14	Wiltshire.
B.B. 46524	23.8.13	Lincolnshire.	–.6.15	Norfolk.
B.B. Z1430	27.8.23	Buckinghamshire	30.6.25	Sussex.

TABLE D

ANALYSIS OF RECOVERY RECORDS OF STARLINGS CAUGHT AND MARKED IN GREAT BRITAIN IN WINTER (OCTOBER–MARCH)

(Excluding birds marked on migration at lighthouses, for which see Table E

Year of Bird's marked Life (dating from 1st October of winter of marking)	Recovered at or near place of marking		Recovered at a distance	
	October-March	April-September	October-March	April-September
First year . .	70	53†	5	3
Second year . .	116	20	1	1
Third year . .	38	8	3	2
Fourth year . .	16	5	2	—
Fifth year . .	5	2	—	—
Total . .	245	88	11	6

Grand Total: 350 records, representing 338 individuals.

Twelve birds recorded twice each in different years or seasons.

† Three reported as nesting.

have bred at the same place in four successive seasons, and to have had two broods in one of them.

The records of immature Starlings caught in late summer, given in Tables C and CC, have been treated separately because these young birds may not have been native to the place of marking; the very early movements of birds

TABLE DD

(Details of cases in Table D, columns 4 and 5)

PARTICULARS OF STARLINGS MARKED IN WINTER AND RECOVERED AT A DISTANCE

Ring No.	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
B.B. C234	1.2.11	Berkshire.	20.2.11	Kent.
B.B. 16078	19.1.12	Berkshire.	2.2.12	Essex.
B.B. 83913	18.10.14	Berkshire.	5.1.15	Middlesex.
B.B. 42342	26.10.13	Northumberland.	3.2.14	Dumfriesshire, Scotland.
B.B. 89578	14.12.16	Kent.	4.2.17	Cambridgeshire.
A.U. 167B	24.12.10	East Lothian, Scotland.	6.2.12	Co. Durham.
B.B. 11125	15.10.10	Lincolnshire.	4.10.12	Zwolle, Holland.
B.B. 31	16.1.11	Berkshire.	9.2.14	Friesland, Holland.
B.B. 16196	29.1.12	Berkshire.	8.3.14	Pomerania, Germany.
A.U. 14891	10.2.11	Mid-Lothian, Scotland.	11.3.14	Christiania, Norway.
B.B. 16018	31.1.12	Berkshire.	17.4.12	Helsingfors, Finland.
A.U. 16480	20.3.11	Mid-Lothian, Scotland.	20.4.11	Nordland, Norway (above Arctic Circle).
B.B. 15461	10.11.11	Berkshire.	23.4.12	Ostfriesland, Germany.
A.U. 8536	20.1.10	Aberdeenshire, Scotland.	ca. 20.8.11	Nordland, Norway (above Arctic Circle).
A.U. 16479	18.3.11	Mid-Lothian, Scotland.	5.4.13	Nord-Trondhjem, Norway.
B.B. 46788	18.1.14	Lincolnshire.	29.6.17	near Bergen, Norway.
B.B. 51022	24.1.22	Yorkshire.	22.11.22	Lancashire.

of the year are well known and are indeed confirmed by some of the records of Starlings marked as nestlings (Table AA). As has already been remarked, however, a few immature birds, not specially noted as such by the markers, may be included in Table B. So far as the records can be relied on for the purpose, they confirm the deductions which can be drawn from Tables A, AA, and B: as compared with Table B, there is a greater proportion of birds recovered at a distance, but the figures are probably not large enough to be considered as significant in this respect.

Both on *a priori* grounds and from the results themselves it can be concluded that Table D deals with a mixed population of British native Starlings and of winter visitors from abroad, while of the former some are stationary and others may be migratory within the limits of the British Isles. The records of birds marked in winter and recovered at or near the same places in summer (or both in winter and in summer in a few cases of double records) confirm the results of marking native birds in summer. Of the birds marked

TABLE E

RECOVERY RECORDS OF STARLINGS CAUGHT AND MARKED ON MIGRATION AT BRITISH LIGHTHOUSES

Ring Number	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
A.U. 24753	12.10.13	Lighthouse, Isle of May, Firth of Forth, Scotland.	29.1.14	Co. Antrim, Ireland.
A.U. 37742	23.11.13	St. Catherine's Lighthouse, Isle of Wight.	6.1.14	Guernsey, Channel Isl'ds.
A.U. 31144	13.3.15	St. Catherine's Lighthouse, Isle of Wight.	25.12.16	Staffordshire.
A.U. 498A	23.10.12	Skerries Lighthouse, off North Wales.	ca.10.5.14	Svendborg, Denmark.
B.B. 43749	26.2.14	Galloway Lighthouse, Wigtownshire, Scotland.	26.11.15	Dumfriesshire, Scotland.
B.B. 43750	26.2.14	Galloway Lighthouse, Wigtownshire, Scotland.	early 4.14	Lanarkshire, Scotland.
B.B. 43746	26.2.14	Galloway Lighthouse, Wigtownshire, Scotland.	24.5.14	Isle of Man.

Total : 7 records and individuals.

in winter and recovered at the same places in subsequent winters nothing definite can be said, as there is no evidence to show whether the birds were native to these places or not : similarly, of the birds recovered in winter at a distance, but within the British Isles, it is not possible to say whether they were migrants merely within the area or winter immigrants from the Continent.

The records of Starlings marked in Great Britain in winter and recovered on the Continent in summer give a very interesting indication of the summer area to which at least some of the British winter immigrants are native. The

region indicated includes southern and arctic Norway, Finland and northern Germany. These records are supplemented, moreover, by the Danish record in Table E, and by the records in Table F of Starlings marked abroad and recovered in the British Isles.

The period October to March has been treated as the winter half of the year for the purposes of this paper—a convenient but obviously arbitrary grouping. Four birds

TABLE F

STARLINGS MARKED ABROAD AND RECOVERED IN THE BRITISH ISLES

(So far as ascertainable from published sources)

Ring Number	Date of Marking	Place of Marking	Date of Recovery	Place of Recovery
Helgoland 16166	31.3.14	Heligoland.	–.12.14	Co. Leitrim, Ireland.
Viborg 1031	15.9.04	Viborg, Denmark.	early 3.06	Edinburgh, Scotland.
Viborg 204	7.10.11 (*as immature*)	Viborg, Denmark.	12.11.11	Norfolk, England.
Stockholm 2067	8.6.15 (*as immature*).	Borgsjö, Vesternorrland, Sweden.	1.2.18	Yorkshire, England.
Rossitten F15943	31.5.13 (*as nestling*)	Ribnitz, Mecklenburg, Germany.	Winter'13	Cornwall, England.
Rossitten 108	10.6.09 (*as nestling*)	Wolmar, Livonia.	ca.20.3.11	Yorkshire, England.
Rossitten 4116	10.6.11 (*as nestling*)	Wolmar, Livonia.	26.12.11	South Devon, England.
Rossitten 7043	–.6.12 (*as nestling*)	Wolmar, Livonia.	1.1.14	Yorkshire, England.
Rossitten 24603	3.6.16 (*as nestling*)	Talsen, Courland.	Before 24.3.17	Co. Tipperary, Ireland.
Rossitten 24609	5.6.16 (*as nestling*)	Talsen, Courland.	14.3.19	Co. Tipperary, Ireland.
Moskwa 1889F	–.5.14	Wolmar, Livonia.	5.12.14	Worcestershire, England.
Moskwa 6160F	11.6.13 (*as nestling*)	Wolmar, Livonia.	–.3.16	Cornwall, England.
Moskwa 2768F	–.5.14	Vitebsk, Western Russia.	–.2 or 3.17	Co. Down, Ireland.
D.O.C. –	1.6.20	Northern Jutland, Denmark.	8.1.21	Yorkshire, England.
D.O.C. –	29.5.22	Northern Jutland, Denmark.	6.3.24	Moray, Scotland.
D.O.C. –	1.6.20	Northern Jutland, Denmark.	29.6.22	Lancashire, England.

marked within this period in the British Isles have been recovered abroad at the same season but in subsequent years. The bird recovered in October and the two recovered in March may possibly have been in their summer areas at these times ; or they, and also the February bird, may have found different winter quarters from those of the year of marking or have been, at the time of recapture, at intermediate points in their journeys.

The records given in Table E represent the fruits of marking Starlings at lighthouses. They could, of course, have been included under the general heading of birds caught and marked in Great Britain in winter, but owing to their special interest they have been kept apart. With regard to the four Aberdeen University cases, 498A was obviously a winter visitor, and 24753 not improbably the same ; the other two may have been native birds, but in view of the conclusions already suggested it is of interest that in all the instances of this kind there is at least a possibility that the subjects were winter immigrants. The three *British Birds* cases, marked at the Galloway Lighthouse, are less significant in that the journeys indicated are in any event comparatively short : the case of 43746, recorded in May, south of where it was marked late in February, is curious, especially when compared with 43750, which was marked at the same time and recovered farther north in April.

In addition to the instances of Starlings marked abroad reaching the British Isles, given in Table F, there are other foreign records which may be mentioned as relevant to the movements in the North European area in general. Starlings marked as nestlings in Holland have been recovered in Belgium and in northern and north-western France : one was also, curiously, recovered in East Prussia in a subsequent summer (Van Oort). A Starling marked in northern Jutland, Denmark, in June, has been recovered in its second winter near Cape Finisterre, France (Skovgaard, 1925). Two marked at Viborg, Denmark, have been recovered on the Texel, off Holland, and at Lister, at the southern extremity of Norway, respectively (Mortensen) : three others, according to Weigold, have been recovered on Heligoland. Rendahl has a record of a Starling marked as a nestling in southern Sweden on 7th June and recovered in Holstein on 14th July. Several Starlings marked as nestlings in northern Germany, and the Baltic States have been recovered farther west in Germany, and also in Holland and Belgium ; the early dates of some of these recoveries

are noteworthy, nestlings marked in May being found at a distance in early July of the same year (Thienemann ; and Lucanus). Starlings marked on the Äland Islands, in the Gulf of Bothnia, have been recovered in Sweden and on Heligoland (Palmen). Finally, there is the remarkable case of a Starling (Helsingfors 604) marked as a young bird on 8th June, 1914, at Viipuri, Finland, and recovered before 26th July, 1915, in Aude, southern France—a distance of 1640 miles (Palmen).

In a different category, but of great interest for comparative purposes, are the records of Starlings marked in Central Europe. Thienemann records journeys from Saxony to Portugal, south-western Spain and Morocco respectively ; from Bavaria and Hessen respectively to southern France ; and from the Harz region to northern Spain. Tratz gives a record of a Starling marked in what was Austrian Silesia and recovered in southern Spain. Weigold records journeys from Bavaria to southern France, south-western Spain and Algeria, and from Hessen to south-eastern France. Krüss also gives a record of a Starling marked in Saxony and recovered in winter in south-western Spain, while Tait quotes Loos as having three records showing migration from Bohemia to Portugal, and Schenk has a record of a journey from Bohemia to southern France. Of Starlings marked as nestlings in Hungary, according to Schenk, several have been recovered in Italy, in Tunis, and in Algeria.

Summary and Discussion of Marking Results

(A) Starlings marked in Great Britain as nestlings have been recovered chiefly at or near the places of marking, and that at all seasons of the year. One has reached the north of France in winter ; three have reached Ireland in winter ; others have performed shorter journeys.

(B) The same applies generally to adult Starlings caught and marked in Great Britain in summer (April-September), but no case of movement beyond Great Britain has been recorded.

(C) The same also applies to Starlings caught and marked in Great Britain as immature birds in late summer, one journey to Ireland and a number of shorter journeys having been recorded.

(D) Starlings caught and marked in Great Britain in winter (October–March) have yielded recovery records of four kinds :

(1) Recovered at or near the places of marking in summer, thus providing further examples of stationary native birds.

(2) Recovered at or near the places of marking in winter, and of indeterminate significance.

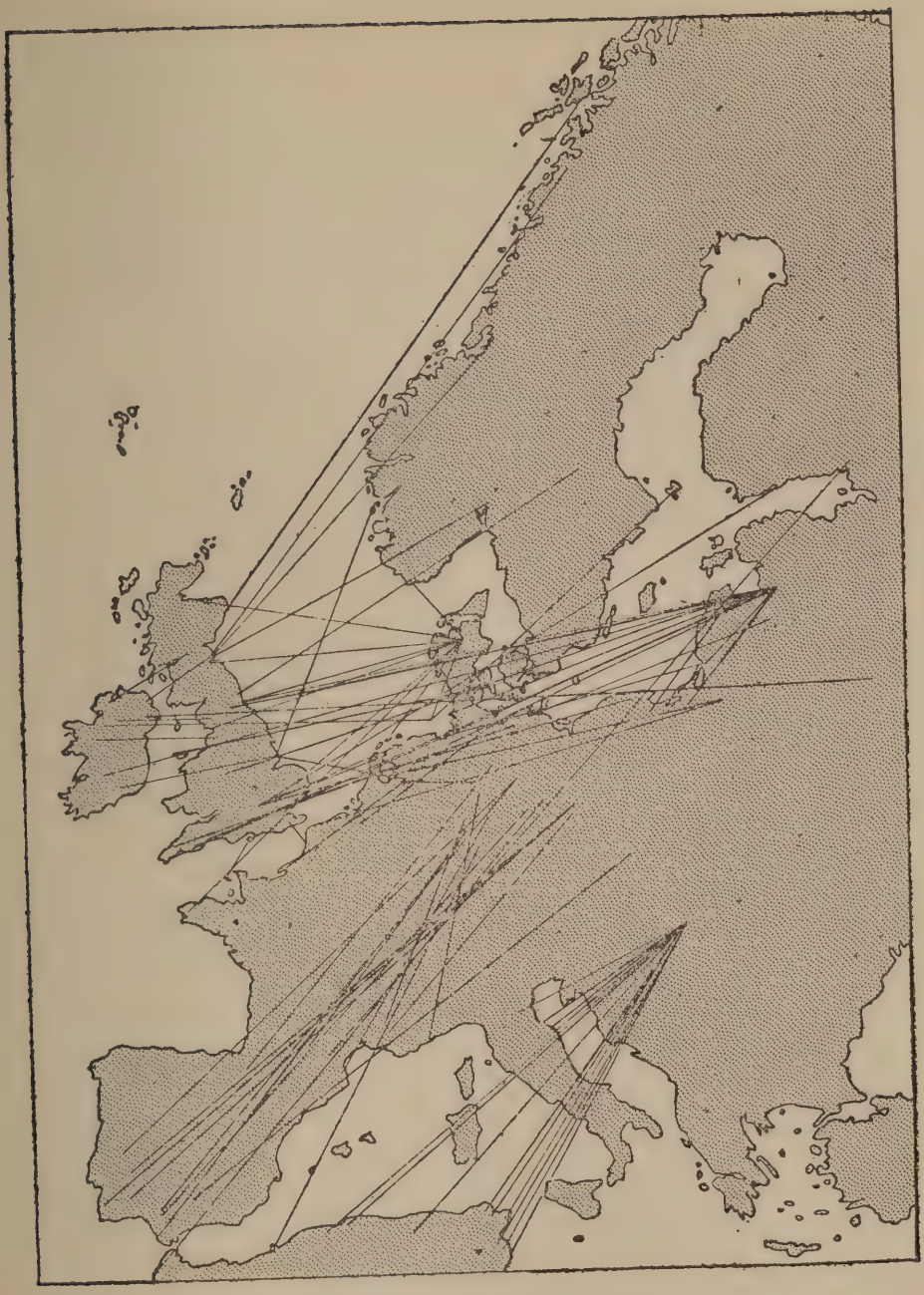
(3) Recovered at a distance in summer, thus indicating the summer quarters, in Norway, Finland, and northern Germany, of Starlings which are winter visitors to Great Britain.

(4) Recovered at a distance in winter, and of rather doubtful significance.

(E) A Starling marked in autumn at a lighthouse in the Firth of Forth was recovered later in the same winter in Ireland ; one marked in November at a lighthouse in the Isle of Wight was recovered later in the same winter in the Channel Islands, while another marked there was recovered in a subsequent winter in the English Midlands ; a fourth, marked in autumn at a lighthouse off North Wales, was recovered in summer in Denmark ; shorter journeys were also recorded in the cases of three birds marked at the Galloway Lighthouse, Wigtonshire.

(F) Starlings marked in summer, mainly as nestlings, in Denmark, Sweden, northern Germany, Courland, Livonia, and western Russia have been recovered in the British Isles, thus confirming and amplifying the records mentioned under (D) (3) above.

Looking at this summary, and comparing it with what is known from other sources about the British migrations of the species, the most striking thing is the almost entire absence of records showing movements of native British birds to France or other countries to the south. The only exception is the case, already cited, of a Starling which crossed from Kent to the Department of Pas de Calais, a journey so short that it would hardly have been taken into account if it had not involved the passage of the Channel. Although Eagle Clarke has said that " Marked native British Starlings have been recovered in winter in France," the present writer cannot trace any other records supporting



MIGRATIONS OF MARKED STARLINGS.

From published data from all sources.

Showing the journeys performed by Starlings (*Sturnus vulgaris*) marked at different times of the year in various parts of Europe. Records not showing long-distance or oversea journeys are omitted.

Each line connects a recovery locality with the corresponding place of marking.

(The lines are NOT intended to indicate the actual routes followed.)

the plural form of the statement. The only other similar journey recorded in the case of a marked Starling appears to be the one shown above in Table E : here again there is little more than the bare minimum of a cross-Channel flight (Isle of Wight to Guernsey), and there is in any event no proof that this bird was native to the British Isles. Too much stress must not, of course, be attached to such negative evidence as the mere absence of records, but it may be noted that the numbers of Starlings marked have been large and the proportion of recoveries considerable, while there are records of Starlings marked elsewhere (and in smaller numbers) being recovered in France, Belgium, Spain, Portugal, Italy, and northern Africa. There is positive evidence, moreover, that native British Starlings are to a large extent either stationary or merely local migrants within the British Isles.

On the other hand, Eagle Clarke's investigations of the movements reported from light-stations, already referred to, led him to the conclusion that there is a southward cross-Channel emigration of Starlings in the late summer and early autumn, before the arrival of the first immigrants from the north-east or east. The cognate Reports of the British Ornithologists' Club Migration Committee, although giving little information as to cross-Channel emigration in the late summer, also tend to show that immigration on the eastern seaboard is not generally observed before the last week in September : but in 1912 large flocks were recorded *going* westwards at Spurn Head Lighthouse, Yorkshire, on the 25th and 29th June, and a further flock on the 19th August, although it is unfortunately not stated whether they were seen *arriving* from the east. The assumption that the early cross-Channel emigrants are native birds, however, is based solely on this absence of observed immigration at the same season ; as this is itself negative evidence, one may fairly argue that it is not necessarily of greater weight than the negative evidence of contrary indication obtained by the marking method. On *a priori* grounds, furthermore, there would seem to be reason to suspect the possibility of some immigration occurring at earlier dates than those generally recorded. Very early movements on the part of young birds of the year are well known in this country, both from the results of marking (*vide supra*) and from observation ; the same is true on the Continent, and it has already been mentioned that nestlings marked in the Baltic States and in northern Germany have per-

formed long westward migrations as early as the beginning of July. On Heligoland the passage of young Starlings is observed in the second half of June and in July, as both Gätke and Weigold have recorded.

Further investigations, it may be concluded, are desirable for the elucidation of this interesting point, about which there seems to be reasonable ground for doubt. From the bird-marking aspect this means (a) the ringing of more native British Starlings, preferably nestlings, to strengthen or destroy the negative evidence already obtained; and (b) the ringing in Scandinavian or other Northern European countries of more Starlings which are native there, to bring to light any early immigration to the British Isles that may possibly exist, and to provide more data for a comparison of the movements of British and Continental Starlings respectively. The Starling is not only a good subject for the marking method, but also one particularly suitable for an international inquiry; it is indeed one of the few species which have already been largely marked, and could be still more largely marked, in all of the European countries in which the method is now in use.

Conclusions drawn from marking results

Many British native Starlings are stationary, while some are migratory within Great Britain or from Great Britain to Ireland: except for one record of a short cross-Channel journey, there is no proof from this source that any of these native birds emigrate to countries abroad. British winter immigrant Starlings come from Denmark, southern and arctic Norway, Sweden, Finland, northern Germany, the Baltic States, and western Russia.

Records of Starlings marked abroad also show journeys from Finland to southern France; from Sweden to north-western Germany; from the Baltic States to northern Germany; from Denmark to Norway, Heligoland and Holland; from northern Germany to Holland and Belgium; from Holland to Belgium and France; from central or southern Germany to southern France, Spain, Portugal, Algeria, and Morocco; from Bohemia to Portugal; from Czecho-Slovakia to Spain and Portugal; and from Hungary to Italy, Tunis, and Algeria.

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For references to sources of single foreign records see end of Chapter XV.

SOURCES OF DATA SHOWN ON MAP.—The map of the migrations of marked Starlings is a revised version of one previously published by the present writer (1922*b*), further records having been added here. Particulars of the records, British and foreign, have been given above, with reference to the sources of the data.

CHAPTER XIII

THE MIGRATIONS OF THE MALLARD AND OF THE PINTAIL

The Mallard, with special reference to the British area: Distribution and British status—Observed movements—Marking in the British Isles—Summary of British results—Foreign results—Conclusion—"Abmigration"—The Pintail: Distribution—Summary of Danish results—Other results—Conclusion.

THE two species of Ducks here selected for special study are subjects of a rather different type from the examples so far discussed. The Mallard, or Common Wild-Duck, will be treated from the point of view of its migrations in the British area, with reference to which many records obtained by the marking method are available. In the case of the Pintail the data to be summarised are those obtained by Mortensen from the marking of birds of this species caught on migration in Denmark; these results constitute one of the most coherent studies of the kind so far achieved, in that they comprise a good number of records all relating to birds of a single species marked under similar conditions.

THE MALLARD (*Anas platyrhyncha*)

With special reference to the British area

The breeding range of the Mallard extends from the Mediterranean northwards through Europe to the Faroes and Iceland but not above the Arctic Circle in Russia, while a distinguishable race is found in Greenland. The species is also found in the Azores, the Canaries, and north-west Africa, and eastwards to Japan, and in North America, especially on the western side. In winter it is also found in Madeira, Egypt, the Persian Gulf, India, Burma, China, Mexico, the West Indies, and Panama.

It is a common resident species in the British Isles, but even more abundant as a winter visitor and bird of passage. According to Eagle Clarke the autumn migration occurs mainly between 12th September and 5th November, passage lasting perhaps until 28th November: the return movement lasts approximately from 25th March to 14th May. In

fine weather the migrants may keep some distance out to sea on our east coast, but onshore storms bring them more into evidence: huge flocks are seen at times. Mallard sometimes strike the lighthouse lanterns on migration.

The question raised by these facts, with regard to the British area, is as to how far our native birds may be migratory, and as to how far the observable movements are rather to be attributed to the winter immigrants. Some answer to this is provided by the following analysis of the relevant marking records which are at present available.

Results of the marking method

The available records are those which have so far been obtained by Witherby under the *British Birds* scheme and those which were obtained by the present writer (1921) during the Aberdeen University Inquiry: the data of the two inquiries, being so similar in nature and referring to the same geographical area, are obviously enhanced in value by being analysed in combined form. Mallard have also been marked in this country independently of the two large scale inquiries, notably by Graham in Cumberland, but there has been no means of including such records as have been obtained in this way. Records of birds marked abroad and recovered in this country have, however, been added—so far as ascertainable from published sources—in the form of supplementary notes, and reference is also made to the principal foreign records relating to the European area as a whole.

Many birds have been marked as hand-reared ducklings, and in some of these cases the eggs have been brought from a distance. These records are here kept apart from those of truly wild ducklings, although a comparison of results does not actually suggest any difference in their behaviour as migrants. When birds have been marked as adults, however, it has obviously been impossible to distinguish between those of hand-reared and those of wild origin. Adults recorded by the markers as being used as half-tame "call ducks" have been excluded altogether, as have all doubtful and incomplete records of any kind.

The following figures for the numbers of birds marked under the *British Birds* scheme are taken up to the end of 1924, with all recovery records received up to the time of completing the list published in the magazine in December, 1925; the corresponding figures for the Aberdeen University Inquiry may be regarded as complete and final in both

respects. Out of 1205 birds marked under the *British Birds* scheme and 425 during the Aberdeen University Inquiry, 173 and 96 respectively have been recovered. The recovery rate is therefore 16·5 per cent over all, but in certain batches the proportion was very high: out of 67 hand-reared ducklings marked in 1912 at Dunecht House, Aberdeenshire, no less than 39 were recovered; and of 38 hand-reared ducklings marked in the same year at Leadenham House, Lincolnshire, 19 were recovered. The high percentage of recoveries for the species may be attributed to the large size of the bird and to the fact that it is both shot for sport and trapped for the market. The fact that the recovery data refer to so large a proportion of the birds marked adds to the value of the results. At the same time it should be noted that there are greater chances of the birds being reported from the places of marking than from elsewhere, owing to the fact that so much ringing has been done on sporting estates and that the markers will never fail to notify recoveries there; shooting at the places of marking may begin, moreover, before much migration could be expected.

Marked as Young Birds.—The records may be summarised as follows:

TABLE A

ANALYSIS OF RECOVERY RECORDS OF MALLARD MARKED AS YOUNG BIRDS IN GREAT BRITAIN

(*The marking locality in forty-two cases was Lancashire, the remainder being scattered throughout Great Britain. One bird marked in Ireland and recovered at the same place is excluded from the table*)

Year of Bird's Life (dating from 1st April of summer of marking)	Recovered at or near place of marking		Recovered at a distance	
	April-September	October-March	April-September	October-March
First year . .	15	36	—	—
Second year . .	1	2	—	—
Third year . .	2	1	—	1
Fourth year . .	—	1	—	—
Fifth year . .	—	—	—	1
Total . .	18	40	—	2

Grand Total: 60 records and individuals.

The two birds recovered at a distance were (B.B. 31245) marked on 20th July, 1911, in Lancashire, and recovered on 31st January, 1914, in Norfolk, and (B.B. 37713) marked on 22nd May, 1918, in Lancashire, and recovered on 2nd November, 1922, in Co. Down, Ireland.

Marked as Young Birds, Hand-reared.—The records may be summarised as follows :

TABLE B

ANALYSIS OF RECOVERY RECORDS OF MALLARD MARKED AS HAND-REARED YOUNG BIRDS IN GREAT BRITAIN

(*Most of the marking localities fall into two groups, namely, sixty-nine birds marked in Aberdeenshire and fifty marked in Essex, Norfolk, and Lincolnshire*)

Year of Bird's Life (dating from 1st April of summer of marking)	Recovered at or near place of marking		Recovered at a distance	
	April-September	October-March	April-September	October-March
First year . .	41	67	—	—
Second year . .	7	10	3	—
Third year . .	1	—	—	—
Fourth year . .	—	—	1	—
Eleventh year .	—	—	—	1
Total . .	49	77	4	1

Grand Total : 131 records and individuals.

The bird reported in its eleventh winter (A.U. 19475) was described as a drake. The ring had worn very well, and was still perfectly strong and legible despite the long period which had elapsed.

Marked as Adults in Summer.—Of adult Mallard caught and marked in Great Britain in summer, 1 was recovered in its first summer, 1 in its second summer and again in its second winter, 4 in their first winter, 1 in its third winter, and 1 in its seventh winter, all at or near the respective places of marking ; a total of 9 records and 8 individuals. (The record of the bird which survived until the seventh

year is for Northumberland, the others are for Berkshire, Warwickshire, and Staffordshire.)

TABLE BB

(*Details of Cases in Table B, columns* 4 *and* 5)

PARTICULARS OF MALLARD MARKED AS HAND-REARED YOUNG BIRDS IN GREAT BRITAIN AND RECOVERED AT A DISTANCE

Ring Number	Date and Place of Marking	Date and Place of Recovery
A.U. 16020	Summer, '10 Aberdeenshire.	18.7.11 Gottrup, Aalborg, north Denmark (*female with brood*).
B.B. 32431	14.6.12 Norfolk.	4.8.13 near Bouchain, Nord, France.
B.B. 9147	26.5.10 Essex.	16.8.11 near Danzig.
A.U. 16066	Summer, '10 Aberdeenshire.	10.8.13 Osterley, Upland, Sweden.
A.U. 19475	3.8.12 Aberdeenshire.	ca. 12.22 Co. Antrim, Ireland.

Marked as Adults in Winter.—The records may be summarised as follows:

TABLE C

ANALYSIS OF RECOVERY RECORDS OF MALLARD CAUGHT AND MARKED IN GREAT BRITAIN IN WINTER

(*Most of these birds were marked in Wigtownshire*)

Year of Bird's marked Life (dating from 1st October of winter of marking)	Recovered at or near place of marking		Recovered at a distance	
	October-March	April-September	October-March	April-September
First year . .	8	3	—	7
Second year . .	33	—	6	1
Third year . .	7	1	—	—
Fourth year . .	—	—	—	—
Fifth year . .	1	—	1	—
Seventh year .	—	—	—	1
Total . .	49	4	7	9

Grand Total: 69 records and individuals.

Marked Abroad and recovered in the British Isles.—According to Palmen a Mallard (Helsingfors 22) marked as a young bird on 17th June, 1913, at Osternotten, Finland, was recovered on 10th December, 1913, in Caithness, Scotland. According to Van Oort one (Leiden 31232) marked as a young bird on 5th July, 1921, at Westpolder,

TABLE CC

(*Details of Cases in Table C, columns 4 and 5*)

PARTICULARS OF MALLARD MARKED AS ADULTS IN WINTER IN GREAT BRITAIN AND RECOVERED AT A DISTANCE

Ring Number	Date and Place of Marking		Date and Place of Recovery	
B.B. 37384	28.2.21	Wigtownshire.	12.5.21	Faroes.
B.B. 36682	27.2.15	,,	1.8.15	near Amäl, S. Sweden.
B.B. 37391	28.2.21	,,	1.8.22	Lake Vänern, S. Sweden.
B.B. 37363	28.2.21	,,	4.8.21	near Gefle, S. Sweden.
B.B. 34819	28.2.14	,,	12.8.14	Norrbotten, N. Sweden.
B.B. 34820	28.2.14	,,	17.8.14	Kaskö, Finland.
B.B. 20534	3.3.22	,,	–.8.22	Kvevlaks Wasa, Finland.
B.B. 34850	28.2.14	,,	–.8.20 (or 21 ?)	Sysmä Gut, Rajala, Finland.
B.B. 37389	28.2.21	,,	23.9.21	Norrköping, S. Sweden.
B.B. 20501	5.3.24	,,	25.10.24	Overijsel, Holland.
B.B. 34842	28.2.14	,,	–.10.17	Hasslö,S.Sweden.
B.B. 20506	5.3.24	,,	–.10.24	Aberdeenshire, Scotland.
B.B. 34853	28.2.14	,,	14.11.14	Scania, S. Sweden.
B.B. 34805	28.2.14	,,	26.11.14	Friesland, Holland.
B.B. 34872	28.3.16	,,	31.1.17	Co. Antrim, Ireland.
B.B. 32636	28.2.13	,,	–.11.13	Räneä, N. Sweden.

Holland, was recovered on 4th February, 1922, at Lowestoft, Suffolk.

Other European Records.—According to Thienemann, young birds marked in the Baltic States have been recovered in winter in northern Germany, Belgium, and north-

eastern France, and others marked in East Prussia have been recovered in winter in Saxony and Moravia: a bird marked in Silesia in March was recovered in Switzerland in the following December. Van Oort records that some adults marked in summer in Holland have been recovered in north-eastern France in winter, and others in southern Germany in a subsequent summer; and that adults marked in Holland have been recovered in summer in Schleswig-Holstein, Sweden, and Finland, and in autumn in Sweden.

American Records.—This species has also been marked in North America, and, indeed, on a very large scale that has already provided some hundreds of records. The marking has been done chiefly in Illinois in spring, autumn, and early winter, and in Missouri in winter and spring. The recovery records given by Lincoln show migration down the Mississippi valley to the coast of Texas and Louisiana, and much less frequent wanderings eastwards towards the Atlantic seaboard: northwards into Canada, the records extend to central Manitoba, Saskatchewan, and Alberta.

Birds marked in Ontario in autumn have also reached Florida and Louisiana on their southward migration.

These American records are not further dealt with in the following summary.

Summary of marking results

Mallard marked in Great Britain in summer, whether as wild young birds, as hand-reared young birds, or as adults, have been recovered mainly at or near the respective places of marking, and the high proportion of recoveries to the total of birds marked gives special validity to the conclusion that most of our native Mallard are strictly stationary: only three birds, marked as ducklings, were recorded elsewhere in the British Isles. Four, marked as hand-reared ducklings, were recovered abroad, namely, in north-eastern France, northern Denmark, north-eastern Germany, and Sweden, but it is noteworthy that all these were reported in summer, *i.e.* at the same season as that in which they were marked in Great Britain in a previous year; in one case a native British Mallard was definitely reported as breeding in the foreign locality. In view of the fact that there is no evidence supporting—and much evidence against—the supposition that there is any ordinary migration on the part of our native Mallard, these exceptional cases seem best explained by the theory that the birds

emigrated in spring in company with foreign birds with which they had chanced to become associated in this country during the winter: the point is discussed more fully below.

The records of Mallard marked in winter are chiefly of interest in so far as they indicate the summer quarters of the birds which are winter visitors to the British Isles. There are five summer records of this kind from Sweden, two from Finland, and one from the Faroes. (There is none from Norway, which seems noteworthy.) These records are supplemented by a record of a bird marked in Finland in summer and recovered in Scotland in winter. There are also three records from Sweden and one from Finland for the early winter months: these possibly refer to birds remaining late in their summer area. Mallard marked in Great Britain in winter were recovered in subsequent winters in Ireland and Holland (two) respectively.

"Abmigration"

There are four records (to which may be added some for other species of Ducks mentioned in Chapter XV), which show that a bird may be born in Great Britain and yet be found—and even found breeding—in a subsequent summer in a totally different area. This is contrary to the generally accepted belief as to the behaviour of migratory birds, and contrary also to the results gained by the marking method in the case of other species than the Ducks, yet it cannot fairly be described, in the face of so many records, as altogether abnormal; rather it would seem to be an irregularity which is to some extent characteristic of the Ducks. At first sight the phenomenon appears to be capable of explanation in either of two ways. Perhaps the more obvious explanation would be that these birds had emigrated from Great Britain in autumn and had failed to find the same route and the same summer quarters in the subsequent spring. But in the case of the Mallard, at any rate, this theory does not seem to be tenable, for there is an entire absence of records indicating an autumn emigration on the part of native British birds, and, indeed, a strong positive case for supposing these to be strictly stationary apart from the extraordinary movements in question. The second explanation accordingly seems to be the more likely, namely, that these birds which find new summer quarters do so by accompanying winter visitant birds which are

returning thither in spring in their ordinary course; the gregarious habits of the Ducks lend further plausibility to this theory. If this exceptional type of movement be so frequent among the Ducks as the records now considered seem to indicate, it may be convenient to introduce a new name to denote its special character. The present writer (1923) has accordingly suggested that the term "abmigration" might be used to describe northward departure in spring, for a new summer area, on the part of birds which had made no corresponding southward journey in the previous autumn. It may be added that the existence of this factor, and the possibility of its occurrence in other cases than those which can be clearly proved, introduces an element of uncertainty into the interpretation of marking records for these species. For example, a Duck marked as a young bird in Great Britain might be recovered in its second autumn in Holland and thus apparently suggest an immigration from Great Britain to Holland; but it might really indicate emigration from Sweden on the part of a bird which had "abmigrated" from Great Britain in the intervening spring.

The Pintail (*Anas acuta*)

A second example from among the Ducks may advantageously be taken because of the existence of a very interesting series of records for the Pintail obtained by Mortensen (1914). The species breeds in the northern countries of Europe, from Iceland and the shores of the White Sea to Holland, Denmark, and northern Germany, and, more sparingly, as far south as the British Isles, Roumania, and Spain: it also inhabits similar latitudes in Asia and North America. In winter it reaches northern Africa, the Sudan, Arabia, India, Ceylon, the East Indies, Japan, Hawaii, Costa Rica, Porto Rico, and Cuba. In the British Isles it breeds only in small numbers, and it is better known as a winter visitor and most of all as a bird of passage.

In the autumns of 1908, 1909, and 1910 Mortensen was able to mark 320 birds of this species caught and released at a duck-decoy on the island of Fanö at the south-western corner of Denmark. Of these no less than sixty-seven, or over 20 per cent, were recovered, two of them twice and most of them at a distance from the place of marking. Of these sixty-nine records it will be of interest to give a summary.

Birds were recovered in their first winter (October–March) as follows :

October : Region of marking (4).
November : Region of marking ; Scotland ; Holland.
December : Holland ; northern France.
January : Western France ; eastern Spain.
February : Holland ; western France ; eastern Spain.
March : Western France ; northern Italy (3).

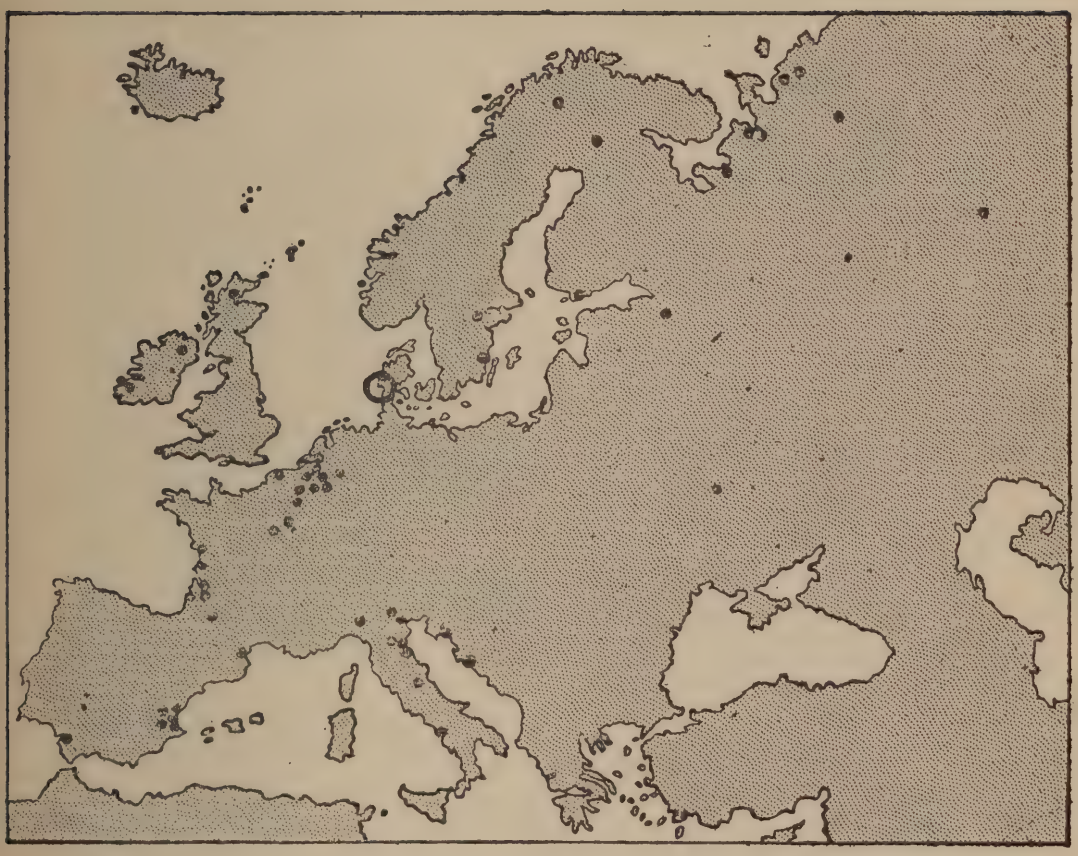
In subsequent winters birds were recovered as follows :

October : Region of marking (6).
November : Western France (2) ; eastern Spain.
December : Southern Ireland ; Holland ; western France ; eastern Spain.
January : Holland ; northern Italy.
February : Holland ; northern France ; southern France ; northern Italy ; Croatia.
March : Holland (2) ; northern France (3) ; northern Italy (2) ; southern Italy ; Dalmatia ; southern Spain.

The records are here separated in this way because it is not necessarily the case that the birds recovered in subsequent winters, otherwise than in the region of marking, had travelled again by way of Denmark instead of by some other route from their summer quarters. No significant difference, however, is apparent. (For convenience four records described as "autumn" have been classed as October records, and two described as "March or April" as March records.) The extreme points reached in winter, according to the records, are County Clare (Ireland), near Cadiz (Spain), near Naples (Italy), and near Spalato (Dalmatia).

Birds were recovered in summer (April–September) as follows :

April : Northern Ireland ; southern Finland ; eastern Russia.
May : Region of marking ; western Russia ; northern Russia (4).
June : ——
July : Region of marking (2) ; south-western Russia ; northern Russia (2).
August : Region of marking ; northern Finland ; southern Sweden.
September : Northern Finland ; southern Sweden ; ~~western France.~~ region of marking.



MIGRATIONS OF MARKED PINTAIL.

After Mortensen.

Showing the localities of recovery, at all seasons of the year, of Pintail (*Anas acuta*) caught and marked while on autumn migration at the island of Fanö, at the south-western corner of the Danish mainland. Records from within a short distance of the place of marking, which include several for subsequent passage seasons, are omitted.

Each black spot indicates a recovery locality. The circle has the place of marking as its centre.

The April record from Ireland, with perhaps some others of the above, may probably be regarded as referring to migration rather than to summer habitat: the same may apply to the April record from Eastern Europe, east of the Ural Mountains, in 59° 51′ E. long. Apart from these cases, the extreme points of the summer distribution indicated by these records are near the coast of the Arctic Ocean in 67° 36′ N. lat. and 52° 30′ E. long., and northern Finland in 68° 27′ N. lat.

The conclusion to be drawn is that Pintail passing through Denmark in autumn come from a summer area which extends to northern Russia as far as the White Sea and the Arctic Ocean, and includes Finland and Sweden. In winter they migrate by way of Denmark, the British Isles, Holland, and northern France, as far as western and southern France, eastern and southern Spain, northern and southern Italy, and the eastern coast of the Adriatic Sea. The distribution of the records is shown on the accompanying map.

Other European Records.—Apart from Mortensen, there are no very important records for this species. Weigold and Krüss mention three Pintail marked in autumn on Sylt, North Frisian Islands, and recovered in Holland in winter. Witherby has two records of Pintail marked in the British Isles, and recovered at the same localities in circumstances of no special interest.

American Records.—The North American form of the Pintail is subspecifically separated from *Anas acuta acuta* under the name of *A. acuta tzitzihoa*. Lincoln has given details of birds marked in Illinois, chiefly in spring and autumn, and recovered southwards as far as Lousiana and Texas and northwards to Saskatchewan and Alberta.

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PINTAIL

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For references to sources of single foreign records see end of Chapter XV.

SOURCE OF DATA SHOWN ON MAP.—The map of the migrations of marked Pintail has been merely redrawn from a map originally published by Mortensen (1914) and based on his own data.

CHAPTER XIV

THE MIGRATIONS OF THE HERRING-GULL AND LESSER BLACK-BACKED GULL

Contrast between migrations of two similar species—Distribution and British status of the two species—Marking of these in the British Isles—The Herring-Gull: British marking results—Foreign results—The Lesser Black-backed Gull: British marking results—Foreign results—Conclusions and comparisons—Dispersal and true migration movement.

THESE two species of Gull can with advantage be treated together, because they provide an interesting contrast. The two birds are of similar size and general habits, but differ notably in the nature and the extent of their migrations. As regards the marking method, both have been marked in the British Isles under similar conditions and in fair numbers: they are therefore likely to have been recovered in about the same proportion of cases and in ways which will make the results closely comparable.

The typical form of the Herring-Gull (*Larus argentatus argentatus*) breeds on the Atlantic, English Channel, North Sea, and Baltic coasts of Europe, and in Greenland and parts—principally in the east—of northern North America. In winter it reaches the Mediterranean Sea (rare), the West Indies, and the Gulf of Mexico. In the British Isles it breeds on most parts of the coasts which are suitable, and it remains common in winter.

The Lesser Black-backed Gull (*Larus fuscus*) breeds in Northern Europe from the White Sea, Lakes Ladoga and Onega, Finland and Scandinavia, to the Faroes, the British Isles, and the west coast of France: it is also said to breed at one point off Morocco and in the Azores. In winter it ranges to the Mediterranean, Egypt, Morocco, the Canaries, Senegal, and Bomy, and visits the Red Sea and the Persian Gulf. The birds breeding in Scandinavia and Russia, and having the more easterly part of the winter range, have been subspecifically distinguished, in one or more forms, from the race native to the British Isles (*L. f. affinis*). In the British Isles the species is scarce on the south coast of England and up the east coast except on the Farne Islands,

but it is common in the Scottish isles, down the west coast of Great Britain, and in parts, even inland, of Ireland. There is a regular southerly movement in autumn and the northern coasts of the British Isles are practically forsaken in winter.

The migrations of Gulls are not easy to observe, and are as a rule hard to distinguish from the mere local wanderings in quest of food which are always taking place. Apart, therefore, from what may be deduced from seasonal variations in numbers and from seasonal extensions of range, one is peculiarly dependent in these cases for information of the kind which the marking method yields. Some account of this, as regards the two selected species may accordingly now be given.

The principal data to be dealt with are the results obtained by Witherby for both species and by the present writer (1921) for the Herring-Gull. The numbers of birds marked and recovered in these two investigations are as follows :

	Marked	Recovered	Recoveries per cent
Herring-Gull :			
British Birds . . .	590	16	2·7
Aberdeen University .	461	25	5·4
	1051	41	3·9
Lesser Black-backed Gull :			
British Birds . . .	4506	170	3·8
Aberdeen University .	44	—	—

The *British Birds* figures are for birds marked up to the end of 1924, and for birds recovered up to the time of completing the list published in the magazine in December, 1925 : the Aberdeen University figures may be regarded as final and complete in both respects. A few recovery records have been excluded from the figures, and from further consideration, on account of imperfection or uncertainty. These include some cases in which the marker admitted strong doubt as to the species, and in which the recovered bird was not obtained for identification. It must be mentioned, however, that a very slight element of doubt as to the species applies generally to a large part of the records here ascribed to the Lesser Black-backed Gull. Very many of the birds were marked as chicks at a nesting colony at Foulshaw, Westmorland, where there were stated to be a few pairs of Herring-Gulls nesting on the same ground. For various seasons which are material for the

present purpose, the numbers of Herring-Gulls in the colony were estimated at from two to twenty-five pairs, at the worst a very small admixture to a large colony of the other species (*fide* H. W. Robinson, the principal marker). As the chicks cannot be distinguished, a possible source of slight error is introduced: it is entirely insufficient to invalidate the general picture presented by the results, but it constitutes a special reason for laying no stress on isolated records which appear to be exceptional. To select for exclusion for this reason such records as are apparently exceptional would, however, be to beg the question as to the migratory behaviour of the species, and the data are in this respect, accordingly, presented as they stand.

It will be observed that the recovery percentage is nearly the same for the two species. One would have expected a rather higher figure in the case of the Herring-Gull, as the chance of hearing of recoveries in the British Isles, from which this species scarcely wanders, should be greater than the chances of hearing of recoveries abroad. (That so many of the Portuguese recoveries of Lesser Black-backed Gulls were brought to light was largely due to the active inquiries of W. C. Tait in that country.) The variation between the two sets of Herring-Gull figures, however, warns one not to stress a point of this kind except when dealing with a very large experience.

The Herring-Gull (*Larus argentatus*)

Of the Herring-Gulls which were marked as nestlings and subsequently recovered, most fall under two headings, namely, those marked on the Aberdeenshire coast and those marked on the east coast of Ross-shire and Caithness. The results may be summarised in tabular form, as on the next page.

(From this summary there has been excluded one Ross-shire bird found at the same place in December, but thought to have been dead for some months. Two of the Aberdeenshire records refer to a single bird, which was caught in Lancashire in January of its first winter, released six weeks later, and recorded in Nairnshire in August two years afterwards.)

Other records of Herring-Gulls marked as nestlings, but not falling within the two series dealt with, are as follows: one marked in the Outer Hebrides and recovered there in December of its first year, one marked in Berwickshire and

TABLE A

SUMMARY OF RECOVERY LOCALITIES OF HERRING-GULLS MARKED AS NESTLINGS IN THE NORTH OF SCOTLAND

(*Records subsequent to the bird's first season are shown in italics*)

Month of Recovery	Marked in Aberdeenshire (Aberdeen University)	Marked in Caithness and Easter Ross (*British Birds*)
July . .	—	*Ross-shire.* *Co. Waterford, Ireland.*
August .	Banffshire *Nairnshire*	Ross-shire. Banffshire. Aberdeenshire.
September .	Aberdeenshire Aberdeenshire Co. Durham Yorkshire Lincolnshire Monmouthshire Heligoland	Aberdeenshire. Calais, France. *Yorkshire.*
October .	Fifeshire Fifeshire Lincolnshire Norfolk	Argyllshire. Lanarkshire.
November .	*Co. Durham* *Yorkshire*	—
December	—	—
January .	Lancashire	Inverness-shire.
February	Norfolk	—

recovered there in the following summer, and three marked in Wales and recovered in their first winter—two in December at short distances from the place of marking, and one in January in Co. Dublin, Ireland.

Taking all these records together and considering the distances travelled and the dates of recovery, the following analysis of the records expresses the chief facts in simple form.

TABLE B

ANALYSIS OF RECOVERY RECORDS OF HERRING-GULLS MARKED AS NESTLINGS IN GREAT BRITAIN

(Figures for records subsequent to the bird's first season are shown in brackets)

	Distance from place of marking			Total
	0–200 miles	200–400 miles	400–600 miles	
July	(1)	—	(1)	2
August	4(+2)	—	—	6
September	4	2 (+1)	3	10
October	4	2	—	6
November	(1)	(1)	—	2
December	3	1	—	4
January	1 (+1)	1	—	3
February	—	1	—	1
	21	9	4	34

There remains a series of records of Herring-Gulls marked otherwise than as nestlings. This is the outcome of the marking of eighty-six full-grown birds which were caught at night on the seashore near Aberdeen, ringed on the spot and released, by the late L. N. G. Ramsay, the late A. G. Davidson, and the writer: this was achieved by approaching the birds with bright lamps. The series is not a large one, and it will suffice to give the following particulars of the recoveries, all of which refer to birds marked in either September or October, 1910.

TABLE C

PARTICULARS OF HERRING-GULLS MARKED IN ABERDEENSHIRE IN AUTUMN (1910) AND SUBSEQUENTLY RECOVERED

"A.U."	Date of Reappearance	Locality of Reappearance
15901	15.11.10	Aberdeen.
16075	20.5.11 (and released)	Burray, Orkney.
	11.1.13	nr. Aberdeen.
10506	26.6.11	Aberdeen.
16017	7.3.12	Aberdeenshire.
10589	6.5.12	Asaa, east coast of Jutland, Denmark.
15985	27.6.13	Gera, Thuringia, Germany.
15891	28.4.14	Caithness.

It is more than probable that the birds marked in this group represented a mixture of native Aberdeenshire birds, of birds from more northerly parts of Scotland, and of visitors from the Continent. The recovery records themselves suggest this, but no further conclusion can safely be drawn. The approximate distances to Asaa and to Gera, are, respectively, 485 and 730 English miles: this last figure represents the longest journey recorded for the species on this side of the Atlantic.

Foreign records

Skovgaard has published an excellent series of records for the Herring-Gull. From 1917 to 1921 nestlings to the number of 1177 were marked in a colony on the island of Fanö, near Esbjerg, at the south-western corner of Denmark. Of these, exactly one hundred, a large proportion, were recovered in the first year of life. The records are all for Denmark and the neighbouring parts of Germany. They include forty-nine birds recovered within a circle of 10 kilometres (*ca.* 6 miles) radius having Esbjerg harbour as its centre, and thirteen more recovered within a slightly wider area taken by Skovgaard as the home region: the remainder were recovered at greater distances, but all within 250 kilometres (*ca.* 155 miles). The following table of the monthly incidence of the records is given:

	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Near place of marking .	6	34	11	6	2	1	1	1	—
At a distance . .	—	5	10	11	—	4	6	1	1

Dispersal took place northwards and southwards in approximately equal degree.

Mortensen had also obtained some records for birds of this species marked in Denmark and these have been published in a posthumous paper. They showed no greater movement than the larger Danish series described above. Van Oort has published records of birds marked as nestlings in Noord Holland: these show no movement farther than to Belgium and north-eastern France, south-eastern England (Kent), and Heligoland. Little movement is shown by the records of birds marked in northern Germany which have been published by Thienemann and by Weigold and Krüss: but one bird marked at Rossitten was recovered two months later in Denmark at a distance of 330 miles. Two Herring-Gulls with Rossitten rings were recovered after eleven and after thirteen years respectively.

From the slight evidence as yet available from the marking of Herring-Gulls in North America, it would seem that the species may be more of a wanderer there. Lincoln records that two marked as young on the New Brunswick coast were recovered, one in winter and one in summer, near New York, while a third was recovered as far away as Texas, in spring. Three birds marked as young on Lake Michigan were recovered in winter in Kentucky, Georgia, and Texas, respectively.

The Lesser Black-Backed Gull (*Larus fuscus*)

The whole of the data of the *British Birds* scheme must relate to the British race, *Larus fuscus affinis*, all the birds having been marked as nestlings in Great Britain. With nine exceptions all the records refer to birds marked either on the Farne Islands, off the coast of Northumberland, or at Foulshaw, Westmorland, each place providing about half of the total of records. (One marked in Cumberland was recovered at the same place, one marked on Ailsa Craig in the Firth of Clyde was recovered in Ayrshire, one marked in Anglesey, Wales, was recovered in the north of England, and of birds marked on the Scilly Isles, off Cornwall, two were recovered in France, three in Portugal, and one in Spain.)

The recoveries took place mainly in autumn and winter and particularly, as usual, in the first few months of the birds' lives. Apart from the six northernmost counties of England, which may be conveniently taken as the native area of the birds, relatively few were recovered in the British Isles: these included five farther south in England and Wales, one (from the Farne Islands) in County Mayo, on the west coast of Ireland, in October of its first year, and one at Grantown-on-Spey, Morayshire, Scotland, in August of its second year. One from Westmorland was, curiously, recovered in September of the year of marking at Haugesund on the west coast of Norway. Attention has already been drawn, however, to the special reason which exists here for laying no stress on isolated records of an apparently exceptional kind.

All the other records refer to southward migration. The series begins with one record from the Gulf of St. Malo, on the Channel coast of France, and then follows, southwards, the west coast of France, the north and north-west coasts of Spain, the coast of Portugal and the south-west

coast of Spain to the Strait of Gibraltar. From there one series continues into the Mediterranean, where there are three records from the south-east coast of Spain, two records from the coast of Algeria, and one record from the northern end of Sardinia. Another series continues southwards, and there are two records from the coast of Morocco and the Rio de Oro, one record from the Canary Islands, and one from St. Louis, Senegal, 16°1′ N. lat. (There is no definite proof that some or all of the birds reaching the Mediterranean did so by way of the Strait of Gibraltar and not, say, by crossing France from the Gironde estuary to the Gulf of Lions, but there is a complete absence of records from any distance inland. The absence of records from out at sea has of course no significance.) The numerous Portuguese records, it may be remarked, are well distributed along the whole coast of that country: an almost complete list of the localities has been published by Tait.

The following table gives an analysis of the records by months and regions of recovery.

TABLE D

ANALYSIS OF RECOVERY RECORDS OF LESSER BLACK-BACKED GULLS MARKED AS NESTLINGS IN GREAT BRITAIN

(*All except nine marked either in Westmorland or on the Farne Islands*)

Month of Recovery	North of England	Remainder of British Isles	Norway	France	Portugal and Atlantic Coasts of Spain	Mediterranean Coasts	West Coast of Africa	Total
May . .	5	1	–	1	–	–	–	7
June . .	2	–	–	–	–	–	–	2
July . .	3	–	–	4	1	–	–	8
August . .	11	2	–	5	–	–	–	18
September .	26	2	1	3	9	–	–	41
October . .	12	2	–	2	16	–	–	32
November .	3	–	–	–	17	2	1	23
December .	2	–	–	–	6	2	1	11
January . .	2	–	–	–	5	1	1	9
February .	–	–	–	1	4	–	–	5
March . .	1	–	–	–	8	–	–	9
April . .	1	–	–	2	–	1	1	5
Total .	68	7	1	18	66	6	4	170

It will be observed that in spite of the good chances of any recoveries being brought to notice there are almost no winter records from the British Isles—three in November, two in December (both at the beginning of the month), and one in January. Attention must again be drawn to the special reason which exists here for not laying stress on isolated records of an apparently exceptional kind, and in any case the proportion of British winter records is quite negligible The absence or great infrequency of British winter records would appear to constitute negative evidence of a kind on which one may safely rely : the infrequency of British summer records, other than in the premigratory period of the first year, has of course to be taken in relation to the small total number of recorded casualties at that season.

Apart from the *British Birds* inquiry, there is a further record of a Lesser Black-backed Gull marked on the Farne Islands under the *Country Life* scheme and recovered in December of its first year in Portugal.

Foreign records

Records of Lesser Black-backed Gulls caught and marked in autumn at Rossitten, at the south-eastern corner of the Baltic Sea, have been published by Thienemann. Many of these birds were recovered at no great distance, usually soon afterwards but in one case after as much as nine and a half years ; of the remainder, some had travelled westwards to as far as Denmark, and others southwards. These last are of special interest. One which was marked (at Hela, near Danzig) in September and was recovered in December in Calabria, southern Italy, may or may not have reached there by way of the Atlantic coasts of Europe, but other records clearly indicate the occurrence of overland journeys. One bird was marked in October and recovered a month later at Plauen, Saxony, 470 miles south-westwards : another was marked in November and recovered thirteen days later at Saromberke, south-eastern Hungary, 620 miles southwards : and another was marked in early November and recovered twenty-two days later at Belgrade, Serbia, 730 miles southwards. Another was marked in October and recovered in the following May at Damietta in the Nile Delta.

There are also a few records of Lesser Black-backed Gulls marked with Rossitten rings elsewhere than in Germany. One marked as a nestling on Öland, Sweden, on 24th June,

1912, was recovered in Essex on 24th February, 1914: two marked as nestlings on Strömö, Faroe Islands, were recovered in winter in Portugal and near Casablanca, Morocco, respectively (Thienemann).

Conclusions

It will be of interest to set out in parallel columns the main conclusions that can be drawn from the foregoing summary of the data for the two species. It is to be noted, however, that in the British Isles the one species has been marked mainly in the north of Scotland and the other in England: it would be useful to have supplementary data for the opposite region in each case.

Larus argentatus	*Larus fuscus*
(1) Herring-Gulls native to the north of Scotland tend to wander southwards in autumn, but within the limits of the British Isles and the immediately surrounding seas. The greatest distance travelled is scarcely 600 miles, the farthest points on record being Co. Waterford, Monmouthshire, Heligoland, and Calais.	(1) Lesser Black-backed Gulls native to the north of England migrate southwards in autumn by way of the coast of France to the Atlantic seaboard of Spain and Portugal and North Africa, as far as Senegal (about 3000 miles), also penetrating the Mediterranean as far as Sardinia. A single record for the west coast of Norway (in September) stands by itself as exceptional. The number recorded in the British Isles in winter is negligible.
(2) The movement shows no special regularity with regard to dates or directions.	(2) The British records become very few after October, and there are also no French records between that month and February. Apart from a single record in July, the records for the Atlantic seaboard of Spain and Portugal cover the period September–March, with the maximum in October and November. Apart from one record in April in each case, the records from the Mediterranean and from the west coast of Africa fall in the period November-January.

(3) The movement appears to have the character of a dispersal: every gradation of distance is shown, and the numbers of records decrease as the distances increase.	(3) The movement appears to have the character of a definite migration. There are few records from what may be called intermediate distances, relatively few birds being recovered in other parts of the British Isles than the area of marking, as compared with the numbers recovered in the area of marking and at greater distances respectively.
(4) Herring-Gulls native to Denmark, Holland, and northern Germany appear to be migratory in even less degree, nearly all the records falling well within 200 miles of the place of marking. The Danish records also very clearly show that the movement is a mere dispersal. Herring-Gulls marked in Scotland in autumn, and possibly native to the Continent, have been recovered in summer in Denmark and in central Germany at distances of 485 and 730 miles. In North America the species is possibly a greater wanderer.	(4) Records of birds marked in autumn at the south-eastern corner of the Baltic Sea indicate that migration takes place both westwards along the coasts and southwards overland to the eastern Mediterranean. A bird native to southern Sweden has reached England, and birds from the Faroe Islands have reached Portugal and Morocco.

The records thus provide further evidence of the different status, as migrants, of the two species. A point of special interest which is brought out is that the movements performed differ not only in degree but also in kind: in the one case there is a mere dispersal and in the other a definite migration. This difference is clearly shown if the numbers of records be analysed according to distance from the point of origin, irrespective of direction or season, in concentric belts of a width, say, of 200 miles each. The number of records for the Herring-Gull falls steadily from belt to belt outwards. The number of records for the Lesser Black-backed Gull falls even more rapidly at first, is low in several succeeding belts, and then rises notably as the region of winter quarters is reached, finally falling away towards the extreme limit of range. This double-peaked curve is typical of true migration: it marks the existence of two distinct seasonal

RECOVERY RECORDS OF MARKED LESSER BLACK-BACKED AND HERRING-GULLS GROUPED ACCORDING TO DISTANCE FROM BIRTHPLACE.

From the data of Witherby and of Thomson.

Showing the numbers of recovery records of Lesser Black-backed Gulls (*Larus fuscus*) and Herring-Gulls (*L. argentatus*) marked as nestlings in Great Britain, grouped according to distance from birthplace.

The curves for the two species represent the numbers of recovery records falling in each belt of 200 English miles measured from the place of birth and marking irrespective of direction or season, and illustrate the difference between a definite migration with its double-peaked distribution and a mere dispersal with its steady diminution of records outwards.

(For the Lesser Black-backed Gull 170 records were available; for the Herring-Gull there were only 34 records, and each record for this species has accordingly been taken as equivalent to five of the other, thus giving the exactly comparable total of 170 for purposes of analysis.)

areas with an intervening tract which provides few records and which may therefore be supposed to be speedily traversed.

REFERENCES

This chapter is largely based on a paper previously published by the author (1924), *but the original references are here repeated.*

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For references to sources of single foreign records see end of Chapter XV.

SOURCES OF DATA SHOWN ON DIAGRAM.—The diagram dealing with the distribution of the recovery records of the Lesser Black-backed Gull and Herring-Gull is a revised version of one already published by the present writer (1924), more recent records having been here incorporated. The data are his own and Witherby's records for the two species, which have been summarised in Tables A, B, and D above.

CHAPTER XV

GENERAL RESULTS OF THE MARKING METHOD

Results relating to particular species and particular areas, and results of more general importance—Distances covered—The relation of particular summer areas to particular winter areas—Directions of migration—Routes—Different types of migration—Differences between birds of the same species inhabiting different areas—Individual migration—Return to former summer quarters—"Abmigration"—The migration of young birds—Return to former winter quarters—Velocity of migration—Gregariousness—Separate migration of old and young.

THE study of bird-migration by the marking method is still in its infancy, and the results so far obtained may be regarded as but a foretaste of what is likely to be achieved. It may nevertheless be useful to conclude this part of the book, devoted as it is principally to the marking method and selected examples of its results, to a brief general survey of the additions to knowledge which have already accrued from this source. These additions may conveniently be grouped under two headings, namely, information as to the migrations of particular species and as to movements in particular areas, and information having a more general bearing.

Detailed studies of several species have formed the subject of the immediately preceding chapters and it is unnecessary to repeat the statements there made: nor can any attempt be made to mention separately the many other species for which interesting results have also been obtained. A systematic account of the various species which have been studied by the method does not come within the scope of this work, and at the present time the attempt would in any event be premature.

It is also not proposed to give details here of the evidence which is beginning to throw new light on the movements taking place in particular geographical regions. It will be sufficient to indicate how the method is notably useful in this regard, taking the British area for the sake of example. As has already been pointed out, it is typical of migration in the British area, which is a "half-way house" in temperate

Europe, that species should be present throughout the year, although known in autumn both as immigrants from the north and east and as emigrants to the south, and *vice versa* in spring. The difficulty is to disentangle the part played by the native individuals of the species, and here the marking method is beginning to fill the gap necessarily left by previous studies of mass movements. Much more evidence is still required, of course, but in the case of the Mallard (Chapter XIII), for instance, there is already a strong presumption that the native birds are stationary and that any southward migration which is observable must therefore be on the part of birds that have already come from more northerly or easterly summer areas. The marking results point to a similar conclusion in the case of the Starling (Chapter XII), although there is some difficulty in explaining all the observed movements on this basis. In other cases, such as those of the Lapwing (Chapter XI) and the Woodcock (*Scolopax rusticola*), the participation of the native individuals in the movements is clearly proved by the marking records.

The purpose of this chapter must rather be to give some survey of the kind of information having a general bearing on the problems of migration, which is beginning to become available as the result of marking. In the first instance mention may be made of some outstanding cases in which great distances have been covered by marked birds. The migration to South Africa of Swallows from the British Isles, and of White Storks from various parts of Europe, has already been dealt with at length (Chapter X). To these cases may be added that of the Common Tern (*Sterna hirundo*), of which species marked birds from East Prussia and from Sweden have been reported in Natal and at the Cape respectively (Thienemann's and Jägerskiöld's rings—*fide* Sclater). In the case of the Sandwich Tern (*Sterna sandvicensis*), also, birds marked in northern Germany, Holland, and the British Isles have been reported from various parts of West Africa, a British and a German bird also reaching Cape Province, and a German bird Natal (Thienemann, 1924*a*; Weigold, 1920*b*; Van Oort; Witherby). Birds of a number of species marked in Europe have been recovered in the north-western parts of Africa, and from Egypt and East Africa there are the records already quoted for the White Stork.

A few marked birds have crossed the Atlantic Ocean. A Kittiwake Gull (*Rissa tridactyla*) marked as a nestling

on the Farne Islands, off the Northumbrian coast, has been recovered in Newfoundland after an interval of a year (Witherby). Black-headed Gulls (*Larus ridibundus*) marked in East Prussia have travelled as far as the Barbados and the east coast of Mexico respectively (Thienemann, 1912*a*, 1916*a*). Two European marked birds, also, have reached the westernmost islands of the Azores group, namely, a Black-headed Gull from Yorkshire (Witherby, 1912*c*), and a Spoonbill (*Platalea leucorodia*) from Holland (Van Oort, 1913*b*). There is, further, the very interesting case of a Common Tern marked as a chick in Maine, United States of America, and recovered near the mouth of the Niger, West Africa, three years later (Lincoln, 1924*a*).

Another Common Tern from the north-eastern United States has been recorded from Trinidad, as also has a Blue-winged Teal (*Querquedula discors*) marked in Ontario, Canada (Lincoln, 1924*a*). There are also three records of Caspian Terns (*Hydroprogne caspia*) marked in Michigan as nestlings and recovered in Columbia, northern South America (Lincoln, personal information).

There is also Menegaux's (1917) interesting case of an Albatross (apparently *Diomedia chinoptera*) marked with a French ring on Kerguelen, as an adult, and recovered in the region of Cape Horn, some 6000 miles distant, almost exactly three years later.

Another long-distance record which may be specially mentioned is that of a Wigeon (*Anas penelope*) marked in England in October and recovered in April, two and a half years later, near Uralsk, about a hundred miles north of the Caspian Sea and just within the boundaries of Asia : the two points are more than 2000 miles apart and practically in the same latitude as each other (Witherby). This may be contrasted with such a journey on a north and south line as that of a Redwing (*Turdus musicus—nec " iliacus "*) marked in Finnish Lapland and recovered in northern Italy (Palmen, 1914).

The chief interest of these records of long migrations, however, is not in the distances covered, which are no greater than some already known from evidence as to the seasonal range of various species, but in the information which they begin to give of the winter quarters of birds native to particular regions of the breeding area of the species concerned. Thus there is now some evidence as to the relation of particular summer quarters to particular

winter quarters. In respect of shorter distances, as has already been shown, there are indications, for instance, of the summer quarters of birds of such species as the Starling and the Mallard, which are winter visitors to the British Isles (Chapters XII, XIII). The records from greater distances similarly give information as to the winter quarters of Swallows breeding in the British Isles and of White Storks which spend the summer in Northern and Central Europe, and so on (Chapter X). Indications of this kind, it is true, can in many cases not be regarded as exhaustive owing to the small chances of obtaining records from, say, Spitzbergen or Central Africa, but so far as the positive information goes it is already of great value. It will be especially interesting when one is better able to compare the winter quarters of birds of the same species inhabiting different summer areas, or *vice versa*, but at present there are few cases in which a particular species has been marked on a large scale in two distinct areas : there are as yet, for instance, no data for a comparison between the migrations of Swallows native to, say, the British Isles, Italy, and Russia respectively.

The marking method is particularly useful in giving evidence as to the general directions of migration. The records confirm but also greatly extend the evidence derived from the observational study of movements at different places, evidence which is necessarily quite local in its application and by no means easy to piece together in the consideration of wide areas. For the sake of example, the directions of the autumn migrations of summer visitant birds breeding in Europe may be considered in the light of some of the new data.

The evidence relating to autumn migration from the British Isles may be conveniently represented by the following table, which shows what species of birds marked here have been recovered in various countries. All the 285 records included refer to individuals known or presumed to be native to the British Isles, usually having been marked as nestlings but occasionally as adults caught in the breeding season. Where not otherwise stated the entries refer only to single records, upon which, of course, too much must not be built ; but for the purposes of a general survey, where species are being taken in the mass, this is not a vital objection. Other entries refer to several or even many records, the number being shown after the name of the species as well as in total after the name of the country. Further

details cannot be given here, but a few of the more important cases have been fully dealt with in earlier chapters.

BRITISH NATIVE BIRDS RECOVERED ABROAD

(*Based on records published up to the end of* 1925.)

Country.	*Species.*	*Authority.*
NORWAY (4)	Teal (*Anas crecca*)	Witherby.
	Gannet (*Sula bassana*)	,,
	Lesser Black-backed Gull (Chap. XIV)	,,
	Guillemot (*Uria aalge*)	,,
SWEDEN (3)	Mallard (Chap. XIII)	Thomson.
	Teal	Witherby.
	Guillemot	Thomson.
FINLAND (2)	Teal	Witherby.
	Tufted Duck (*Nyroca fuligula*)	,,
DENMARK (2)	Mallard	Thomson.
	Teal	Witherby.
GERMANY (6)	Mallard	,,
	Teal	,,
	Sheld-Duck (*Tadorna tadorna*) (2)	Thomson.
	Black-headed Gull (*Larus ridibundus*)	Witherby.
	Herring-Gull (Chap. XIV)	Thomson.
HOLLAND (5)	Robin (*Erithacus rubecula*)	Witherby.
	Wigeon (*Anas penelope*)	Thomson.
	Shoveler (*Spatula clypeata*)	Witherby.
	Gannet	,,
	Black-headed Gull	,,
BELGIUM	Gannet	,,
FRANCE (112)	Starling (Chap. XII)	Ticehurst.
	Greenfinch (*Chloris chloris*)	Witherby.
	Linnet (*Carduelis cannabina*) (4)	,,
	Meadow-Pipit (*Anthus pratensis*) (5)	,,
	Pied Wagtail (*Motacilla alba yarrellii*) (2)	,,
	Spotted Flycatcher (*Muscicapa striata*)	,,
	Whitethroat (*Sylvia communis*)	,,
	Mistle-Thrush (*Turdus viscivorus*) (3)	,,
	Song-Thrush (*T. philomelus*) (6)	,,
	Blackbird (*T. merula*)	,,
	Wheatear (*Œnanthe œnanthe*) (2)	,,
	Whinchat (*Saxicola rubetra*)	,,
	Redstart (*Phœnicurus phœnicurus*)	,,
	Robin	,,
	Swallow (Chap. X) (5)	,,
	House-Martin (*Delichon urbica*) (2)	,,
	Sand-Martin (*Riparia riparia*)	,,
	Mallard	,,
	Cormorant (*Phalacrocorax carbo*) (11)	,,
	Gannet (2)	,,
	Manx Shearwater (*Puffinus puffinus*)	,,

Country.	*Species.*	*Authority.*
FRANCE (*continued*)	Stone-Curlew (*Burhinus œdicnemus*)	Witherby.
	Lapwing (Chap. XI) (9)	Witherby; Thomson.
	Dunlin (*Calidris alpina*)	Witherby.
	Redshank (*Tringa totanus*)	,,
	Common Sandpiper (*T. hypoleucos*)	,,
	Woodcock (*Scolopax rusticola*) (3)	Percy; Witherby; Thomson.
	Sandwich Tern (*Sterna sandvicensis*) (3)	Witherby.
	Common Tern (*S. hirundo*) (3)	,,
	Little Tern (*S. albifrons*)	,,
	Black-headed Gull (*Larus ridibundus*) (15)	Witherby; Thomson.
	Herring-Gull	Witherby.
	Lesser Black-backed Gull (18)	,,
	Land-Rail (*Crex crex*) (2)	Thomson.
SPAIN (29)	Pied Wagtail (2)	Witherby.
	Song-Thrush	,,
	Swallow	,,
	Cormorant (2)	,,
	Gannet	,,
	Lapwing (5)	Witherby; Thomson.
	Woodcock (2)	Douglas; Thomson.
	Common Tern	Witherby.
	Black-headed Gull (2)	,,
	Lesser Black-backed Gull (11)	,,
	Guillemot	,,
PORTUGAL (98)	Tree-Pipit (*Anthus trivialis*) (2)	,,
	Meadow-Pipit (2)	Witherby; Thomson.
	Pied Wagtail (3)	Witherby.
	Chiffchaff (*Phylloscopus collybita*)	,,
	Willow-Warbler (*P. trochilus*)	,,
	Song-Thrush	Thomson.
	Whinchat	Witherby.
	Redstart	,,
	Cormorant	,,
	Gannet	,,
	Turtle-Dove (*Streptopelia turtur*) (2)	,,
	Lapwing (11)	Witherby; Thomson.
	Woodcock	Ardilaun (publ. Witherby).
	Sandwich Tern	Witherby.
	Common Tern (4)	,,
	Little Tern	Thomson.
	Black-headed Gull (5)	Witherby.
	Lesser Black-backed Gull (59)	Witherby; *Country-Life*.

Country.	*Species.*	*Authority.*
SARDINIA	Lesser Black-backed Gull	Witherby.
ITALY (2)	Wood-Warbler (*Phylloscopus sibilatrix*)	,,
	Cuckoo (*Cuculus canorus*)	,,
ALGERIA (2)	Lesser Black-backed Gull (2)	,,
MOROCCO (2)	Lapwing	,,
	Lesser Black-backed Gull	,,
AZORES	Black-headed Gull	,,
CANARY ISLANDS	Lesser Black-backed Gull	,,
RIO DE ORO	Lesser Black-backed Gull	,,
SENEGAL	Lesser Black-backed Gull	,,
IVORY COAST	Sandwich Tern	,,
BELGIAN CONGO	Swallow	,,
ANGOLA	Sandwich Tern	,,
SOUTH AFRICA(8)	Swallow (7)	,,
	Sandwich Tern	,,
NEWFOUNDLAND	Kittiwake Gull (*Rissa tridactyla*)	,,

At least the first five countries in the foregoing list, lying to the north or east of the British Isles, may be excluded from consideration in respect of the directions of migration of true summer visitors. Practically all the records for these countries fall under one or other of two headings. In the first place there are records of Ducks of several species, but these relate not to the migration season but to subsequent summers. In the second place there are records of sea-birds which are subject to irregular dispersal rather than to definite migrations. Both these points will be dealt with more fully at a later stage.

For the rest, it will be seen that the overseas migration of native British birds is almost entirely in a southward direction. Recoveries of summer visitors of Passerine species are recorded only from France, Spain, Portugal, Italy, and Africa, and of these Italy is represented by only one record—to which only one record of a non-Passerine bird can be added. An examination of the French records shows that they are chiefly from the coastal regions, and especially from the southern half of the west coast. There are relatively few records from the centre of France and none from its Mediterranean region : whatever significance the fact may have, almost all the records of Passerine birds from the north coast of France refer to members of the Thrush genus. There are few records of Passerine birds from Spain, but relatively many (as well as large numbers for other species) from Portugal. It must, however, be remembered that the total number of records for Passerine birds is still too small to warrant any definite conclusions.

The Waders and sea-birds, as one would expect, are recorded almost entirely from the coasts.

It is not proposed to give here any similar list of cases in which birds not native to the country—or of doubtful origin—have been marked in the British Isles and recovered in countries to the north, north-east, and east. Most of them have already been cited in the chapters dealing with the Starling and the Mallard, the two species figuring most prominently in this respect. The evidence from this source is complementary to that obtained by the marking in other parts of north-western Europe of birds which are native there, and the question may be most conveniently discussed from the point of view of these countries.

From the northern countries of the European continent the direction of autumn emigration in the great majority of cases is south-westwards and westwards. Mortensen's results from the marking of Pintail (Chapter XIII) have already been described, and a very similar case was established by him in the case of the Teal. The evidence is very clear, also, in the cases of the Starling (Chapter XII) and the Lapwing (Chapter XI), both of which have already been fully described. Another instance is that of the Hooded Crow (*Corvus cornix*), of which large numbers have been caught and marked while on migration at the south-eastern corner of the Baltic Sea : the subsequent winter records lie westwards through northern Germany to north-eastern France, and the summer records northwards and north-eastwards through the Baltic States and part of Russia, to Finland (Thienemann). Records published by Rendahl (1925) of Hooded Crows marked as young in northern Sweden more faintly indicate a parallel course, first running south through southern Sweden and Denmark and then turning westwards to Belgium (two records) and England (Suffolk).

Still another case that may be mentioned is that of Spoonbills native to Holland and recovered in England, France, Portugal, and the Azores (Van Oort). Examples could be multiplied, especially if one includes such isolated records as that of a Red Kite (*Milvus milvus*) marked in Denmark and recovered in Spain (Mortensen, 1907), and that of a Fieldfare (*Turdus pilaris*) marked on the Äland Islands, off the coast of Finland, and recovered in the south-west of France (Palmen, 1914).

Even from Hungary the predominant trend of autumn emigration is south-westwards and westwards. The direction

MIGRATIONS OF MARKED HOODED CROWS.

After Thienemann, adapted.

Showing localities of recovery, at all seasons of the year, of Hooded Crows (*Corvus cornix*) aught and marked, mainly in autumn, while on migration at Rossitten, East Prussia, at the outh-eastern corner of the Baltic Sea. Records from within a short distance of the place of narking are omitted.

Each black spot indicates a recovery locality. The circle has the place of marking as its entre.

in which records most frequently lie is that of Italy and Tunis: the Starling is a case in point (Chapter XII), and another example is provided by the Night-Herons (*Nycticorax nycticorax*) and Squacco Herons (*Ardeola ralloides*) marked in Hungary and recovered in Dalmatia, Italy, Sicily, Malta, Algeria or Tunisia, and Nigeria—the Night-Heron also in Greece (Schenk). In other cases the path seems to continue westwards from northern Italy, through southern France to Spain: the Lapwing provides a good example of this (Chapter XI), and one may also mention the record of a Glossy Ibis (*Plegadis falcinellus*) marked in Hungary and recovered near Seville, south-western Spain (Schenk, 1922).

There is, indeed, a conspicuous relative scarcity of evidence of migration from Northern Europe southwards across the Continent towards the eastern Mediterranean, and only for a few species are records showing movement of this kind commonly obtained. One of the best examples of direct southward migration is that of the Rough-legged Buzzard (*Buteo lagopus*). Young birds of this species were marked in some numbers in northern Sweden and the course traced by the records is southward, sometimes with an easterly trend on the Finnish side of the Gulf of Bothnia, as far as Hungary (Jägerskiöld). It has already been mentioned that some Lesser Black-backed Gulls follow a similar direction from the eastern Baltic (Chapter XIV). There are also some other instances, including such records as that of a Turtle-Dove (*Streptopelia turtur*) marked in Silesia and recovered in Greece (Thienemann, 1914*a*), and that of a Cuckoo marked in Prussian Saxony and recovered in its first autumn on the island of Syra in the Ægean Sea (Weigold, 1925*a*).

The most conspicuous exception, however, is that of the White Storks which are native to Denmark, parts of Germany, and Hungary, and which travel south-eastwards towards Asia Minor. Here, also, there is the especially interesting point that birds from the extreme west of Germany have been shown to travel south-westwards, and one of the most valuable studies that could be made would be a fuller working out, from a larger series of records, of a comparison between the two divergent movements. The available evidence has already been discussed in detail (Chapter X).

In the foregoing paragraphs reference has been made to the directions of migration, and use of the word "route" has been deliberately avoided. A single marking record

MIGRATIONS OF MARKED NIGHT AND SQUACCO HERONS.

From the data of Schenk.

Showing the recovery localities of Night-Herons (*Nycticorax nycticorax*) and Squacco Herons (*Ardeola ralloides*) marked as nestlings at various localities in Hungary (pre-war extent). Records from within a short distance of the area of marking are omitted. The records for localities to the north of the native area are for the late summer of the year of birth: the other records refer to southward migration, winter-quarters or return journey.

● Recoveries of Night-Herons.

✚ Recoveries of Squacco Herons.

The area of marking is roughly indicated by the large cross and circle.

may give two points in the journey of an individual bird, but it gives no certain indication of the path followed between them, which is not, of course, necessarily a straight line, and speculation on the subject is of slight value: where such time has elapsed that the bird is recovered on a journey subsequent to the first after marking, there is obviously still greater room for fallacy in interpretation.

When a movement is represented in the evidence by a large number of marking records, it becomes possible to consider the probable path of flight, but deductions must still be made with very great caution. It is temptingly easy to connect up the record points on a map, to call the resulting line a route, and to proceed to relate this supposed route to various geographical features. Yet it does not follow, for instance, that because some Scottish Lapwings are recovered in Ireland and others in Portugal, the route to Portugal necessarily traverses Ireland: the two countries may be the end-points of two distinct paths. Yet in time the number of records from intermediate points will increase and it will become possible to lay more stress than at present on the negative evidence provided by the absence of records from particular areas, and in this way the existing knowledge of the paths of flight will undoubtedly be greatly enlarged. It is to be noted, that the marking method, from its very nature, is unlikely ever to yield positive evidence as to oversea routes.

Some writers on the Continent, in particular, seem to have gone further than the evidence yet warrants in defining what they believe to be the routes followed by species which have been studied by the marking method. Schenk (1924), for instance, has interpreted the marking results for the Woodcock (*Scolopax rusticola*) in accordance with his theories as to routes, mentioned in a previous chapter, in a way which seems to beg the question at issue. Thienemann and Lucanus, also, appear to lay too much stress on supposed routes in the case of the Black-headed Gull (*Larus ridibundus*): the fact that birds tend to be recorded near coasts and rivers does not, with a partially aquatic species, at all necessarily indicate that these are actually followed in flight; these features would be equally likely to intercept and detain, by their attractions, birds proceeding at right angles to their courses. That geographical features of this kind are indeed followed is not improbable, but it seems undesirable to form early conclusions on the subject: one

MIGRATIONS OF MARKED ROUGH-LEGGED BUZZARDS.

Mainly after Jägerskiöd, with additional data from Thienemann.

Showing recovery localities of Rough-legged Buzzards (*Buteo lagopus*) marked as nestlings in northern Sweden, or as adults caught on migration at Rossitten, East Prussia, at the south-eastern corner of the Baltic Sea. Records from within short distances of the respective places of marking are omitted.

● Recoveries of birds marked as nestlings in northern Sweden.

O Recoveries of birds similarly marked in the same part of Sweden, but with German rings.

✕ Recoveries of birds marked at Rossitten as adults caught on migration.

The circle indicates the area of marking in Sweden. The arrow shows the position of Rossitten.

of the great merits of the marking method is the accuracy of its data, and the study will not advance as it should if this is in danger of being lost amid speculative assumptions. A highly critical interpretation will in the long run be more valuable.

Records of marked birds clearly bring out differences in the types of movement performed by birds of various species, which is a subject of much interest. Thus, a noteworthy point has emerged in the case of several species, namely, the absence of records of marked birds from what may be called " intermediate distances," birds being usually recorded either from their native locality or, alternatively, from a relatively great distance. In these cases, such as the Lapwing (Chapter XI) and the Lesser Black-backed Gull (Chapter XIV), it accordingly seems probable that individual birds are either strictly resident or very definitely migratory, gradations being absent. In other cases, such as that of the Herring-Gull, the records clearly reveal a mere tendency to dispersal, a point which has already been illustrated in the preceding chapter. One may also note, from the table given earlier in this chapter, that while one British Guillemot (*Uria aalge*) reached Spain to the south, others have gone east to Norway and Sweden. Again, there is a record of a Gannet recovered in mid-winter on the Norwegian coast, some 500 miles north of its native locality : others have gone south to France and Portugal.

It is possible that an intermediate type of movement consists of a dispersal with a pronounced directional trend, and that the Black-headed Gull, already mentioned, is an example of this. Very large numbers of birds of this species have been marked in most European countries where the method is in use. Black-headed Gulls bred in East Prussia have been shown to spread over a wide area, some southwards across the Continent towards the Adriatic, some westwards along the coasts of the Baltic Sea and North Sea, and still others across the Continent in the region of the Rhine, the Lake of Geneva, and the Rhone : two cases in which the Atlantic was crossed have already been noted. Birds from other northern countries have been recorded in similar directions, and some from Finland have reached the Mediterranean. Birds marked in Central Europe have travelled not only southwards to the Mediterranean, but also northwards to the North Sea. In discussing a large series of British records, including recoveries from France, Spain, Portugal, and the Azores, Robinson (1915) concludes

that the movement is a scattering with a southward tendency, and this would seem to be a just statement of the position.

Another point is the difference which is shown in the degree to which migration is developed among birds of the same species but native to different areas. The Heron (*Ardea cinerea*), for instance, appears to be a resident or only locally migratory bird in the British Isles, so far as the records go. Herons marked in Denmark, however, have been shown to migrate to Great Britain, France, Spain, and Portugal (Mortensen ; Saxtorph).

Much interest also attaches to what may be called " individual migration." This term is used to express the fact that individual birds belonging to the same species and native to the same area may behave differently as regards migration. The point has been very clearly brought out by the marking method, and in the preceding chapters instances are given where individuals have sought different winter quarters, or where some individuals have been resident while others have migrated. In the case of Lapwings bred in Aberdeenshire and the neighbouring counties, for example, some have wintered there, some in Ireland, and some in Portugal. As has been noted above, however, it remains undecided whether Ireland lies on the way to Portugal or whether there is, indeed, a definite divergence of paths. The theoretical implications of these facts are of great interest, as will be noted in a subsequent chapter.

It remains possible that there may not only be differences between one individual and another in the same area, but that one and the same bird may behave differently in successive years. This the marking method will not so readily show, because evidence on the point would involve the reappearance of a marked bird already once recovered and released, and this can but seldom happen apart from recoveries at a place of marking where systematic trapping is carried out. But while exceptions may easily occur without coming to light, there are already many records which show that migrants return to the same summer quarters or to the same winter quarters with constant accuracy.

Evidence is most abundant as to the return of migratory birds to the same summer quarters. Definite proof of this return, for long presumed on general grounds by most students of migration, has been obtained for a number of wholly summer-visitant species of which birds have been marked, chiefly as nestlings, in the British Isles. The following is a list of these :

Swallow (Chapter X) and Swift (*Apus apus*)—according to Witherby and to Thomson;

Willow-Warbler (*Phylloscopus trochilus*); Wood-Warbler (*P. sibilatrix*); Wheatear (*Œnanthe œnanthe*); Whinchat (*Saxicola rubetra*); House-Martin (*Delichon urbica*); Sand-Martin (*Riparia riparia*); Wryneck (*Jynx torquilla*); Turtle-Dove (*Streptopelia turtur*); and Common Tern (*Sterna hirundo*)—all according to Witherby;

Spotted Flycatcher (*Muscicapa striata*)—according to Thomson.

These examples will here suffice, but several other species—including, of course, the notable case of the White Stork (Chapter X)—could be added if continental records were also drawn upon. Lucanus, indeed, mentions over forty species in this connection, but in certain cases records for subsequent summers are invalidated to a greater or less extent by lack of grounds for the assumption that the individual had left the respective localities in the interval: in the instances named above the species are, of course, unknown in winter in the area of marking. There are also some records for North American birds showing return to previous summer quarters.

The records of the return of summer visitors include records of birds marked in the nest and returning to their birthplace, and records of birds marked as adults and returning to their former nesting-places. In many cases the return is very exact, to the same garden or building it may be, and in other cases the return is to the same district merely. Not only are the positive records already numerous, but there is a notable scarcity of records of birds finding other summer quarters in different districts, and an almost complete absence of records of birds finding new summer quarters at any really great distance from the original locality.

A partial exception to the rule of constancy to the native summer area appears to exist in the case of certain Ducks. There are four records for the Mallard, which have already been given (Chapter XIII). In addition, there are five records of Teal (*Anas crecca*), which were marked as hand-reared birds in Cumberland and recovered in the summers or autumns of subsequent years in southern Norway, northern Sweden, Denmark (2), and northern Germany, respectively (Witherby). A Tufted Duck (*Nyroca fuligula*), also, was marked as a young bird in Northumberland, and recovered in northern Finland in a subsequent summer (Witherby). Again, of Sheld-Duck (*Tadorna tadorna*)

marked as young birds in Hampshire, two were recovered in subsequent summers in north-western Germany (Thomson). A few other cases might perhaps be included, but the data are capable of more than one interpretation. These records show that a Duck may be born in Great Britain and yet be found—and sometimes even found breeding—in a subsequent summer in a totally different area. This has already been fully discussed in the case of the Mallard in a previous chapter, and the writer has tentatively given the name "abmigration" to the phenomenon. It seems to be best explained not by assuming winter migration to the south and return to a different summer area, but by supposing that resident individuals may remain in their native area for the winter, as in the case of British Mallard they normally would, and in spring accompany winter-visitant individuals to the proper summer area of the latter.

With reference to the return of migrants to their former summer quarters, information is needed as to the behaviour of young birds of species in which maturity is not reached for two or more years. In the case of the White Stork (Chapter X) it has already been shown that some immature birds may remain in the winter quarters of the species, or in some intermediate area, while the adults are breeding elsewhere. But there is not yet evidence as to how common this is, or as to how far only immature birds are concerned. The point is one of some theoretical interest, upon which the marking method is likely to throw more light.

Not altogether irrelevant to the question of return to previous summer quarters is the following record of "homing" on the part of a Teal. The bird was caught at Netherby, Cumberland, where it had probably been bred, and was turned down in Essex when full-grown : it was subsequently recovered at Netherby in November of the same year, another of the same lot having, however, reached north-western Germany by August (Witherby, 1911*c*). Birds which have been subject to so much artificial interference must be excluded from the study of migration proper, but the case is of some interest in itself.

Another point related to the question of summer quarters is the tendency shown by some birds, and especially young birds it would seem, to move some distance northwards in the late summer before migrating to the south. This was shown in the case of several Night-Herons marked in Hungary (Schenk, *see above*), and notably in the case of

a Common Tern marked as a chick in Holland and recovered in the same autumn in southern Sweden (Van Oort, 1915*c*). Similarly, a Sandwich Tern marked as a nestling on 15th July on the Farne Islands, off Northumberland, was recovered in the Moray Firth, 155 miles northwards, on 29th August of the same year.

There are far fewer records showing the return of migratory birds to the same winter quarters, or the same points on their line of passage. This follows from the fact that very few birds marked in their breeding localities are recorded from a distance more than once. Records bearing on the point are more likely to be obtained in the case of birds marked in their winter quarters or on migration, as a single recovery in any instance may then suffice. The interest of most of the records of this kind which have so far been obtained in Europe, however, is diminished because they refer to species in respect of which a long journey in the intervening period cannot be safely presumed. It is only by a lucky chance that a bird will be marked in one winter, recovered and released at a distance in summer, and recorded once more at the original point in the next winter : this has occurred in the case of a Herring-Gull (Chapter XIV), but the distance was not very great and the species is by no means a typical migrant.

Fortunately, there is some very clear evidence on the subject from America, where Baldwin and others have done much marking of birds caught in winter quarters in the process of systematic trapping : this particularly refers to marking done so far south as Georgia. White-throated Sparrows (*Zonotrichia albicollis*) and Myrtle-Warblers (*Dendroica coronata*) marked in that southern state in winter may be presumed to be native to Canada or at least to the extreme northern portion of the United States, not less than 600 miles away. Several birds of these species marked in Georgia in winter have been recaptured in the same traps in one or more subsequent winters. The following records for a single White-throated Sparrow, all from the one locality in Georgia, are noteworthy (Baldwin, 1921) :

1916. 5th (marked), 6th, 7th, and 16th March.
1917. 7th and 19th March.
1918. (No trapping done.)
1919. (No trapping done.)
1920. 25th and 27th February, and 2nd, 3rd, 6th, and 22nd March.
1921. 17th, 23rd, 25th, and 27th March.

In the case of both these species the birds may be in the district all winter, although trapping is done there only in the later months.

With what accuracy birds of the year, where these migrate by themselves, find the same winter quarters as their parents is a point of the greatest theoretical importance, as will appear from the subsequent chapters. Evidence upon it, as yet not available, is not beyond the possibilities of the marking method.

It is only by pure accident that the marking method is likely ever to yield records showing the velocity of migration flight, but evidence giving some *minimum* indication of the total length of journey accomplished in a given time is not impossible to obtain. Lucanus mentions some records of young White Storks which have been recovered within a few days of their departure (subsequent to marking in the nest) being observed. The distances covered were 1200 kms. in five days, 1200 kms. in six days, 600 kms. in three days, 500 kms. in three days, and 640 kms. in seven days. The actual period required for the journey may, of course, have been *less* than that which the record gives.

Finally, mention may be made of some interesting records relevant to the question of gregariousness among migratory birds. In the course of his marking of the White-throated Sparrow, already referred to, Baldwin has come to the conclusion that there are "neighbourhood groups," consisting of birds which band together for migration season after season. Whittle and Fletcher, too, have recorded a notable instance of this in the case of the Slate-coloured Junco (*Junco hyemalis*). At a trapping station in Massachussetts, twenty-three of these birds which appeared there after a spell of very hard weather were caught together and marked on 25th January, 1923: some of them were recorded again at various times before their departure in April. From October onwards some Juncos were caught from time to time, but none of these. Then, again after a spell of very hard weather, twelve Juncos were caught together on 4th February, 1924, and six of these were found to be from the party of twenty-three caught together just over a year before.

A cognate point relates to the separate migration in autumn of adults and of young birds of the year, which is believed to be the rule in the case of many species. This is a question of great importance upon which the observational evidence is very far from complete. Further observation

is desirable, but marking may also be of some assistance. So far, the evidence from the marking method is confined to records of very early movement of young birds, as in the case of the Starling (Chapter XII): but the negative evidence for old birds is untrustworthy, because birds have been mainly marked when young and tend to be recovered in greatest number in the early months of life. Many records showing the dates of movement both of young birds and of adults, in a given species, are required before conclusions can be safely drawn from this source.

In the first chapter of this book bird-migration was described as a phenomenon characterised by its vastness, by its complexity, and by its regularity. These points are again brought out by a consideration of the results already obtained by the marking method. In the first place there are the long distances travelled in some cases, and the great number of species which show seasonal movement in some degree. In the second place there are the different types of migration, the differences between one species and another, the differences between individuals of a species native to various areas or even to a single area, and the differences in the dates, directions, and extent of movement. In the third place there are the regularity with which certain features of the migration of a species are maintained and the accuracy with which at least many birds return to their native localities and with which at least some again find the winter quarters of former seasons. One is thus reinforced in the idea that, for all its vastness and complexity, migration, in its most developed forms, is a remarkably regular periodic phenomenon which follows definite laws and is no mere fortuitous or haphazard response to the capricious pressure of varying external factors.

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(*In view of the prominence given to bird-marking in this book, an extensive, although not exhaustive, list of references to the subject is appended to this chapter. For the most part, notice has not been taken of notes on isolated records which can be more conveniently found in collected reports, or of papers making no original contribution to the subject.*)

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The map of the migrations of marked Night and Squacco Herons has been compiled from data published by Schenk (1908–24*a*).

The map of the migrations of marked Rough-legged Buzzards is based mainly on data and maps published by Jägerskiöld (1913, 1914), with two additional records on the authority of Rendahl (1925). To these are here added a few records published by Thienemann (1903–24*a*), including two of birds marked in Sweden with German rings.

PART III

THE MAIN PROBLEMS OF BIRD-MIGRATION

STATEMENT AND DISCUSSION

" We have here more than enough to excite our wonder, and indeed are brought face to face with perhaps the greatest mystery which the whole animal kingdom presents—a mystery which attracted the attention of the earliest writers, and can in its chief point be no more explained by the modern man of science than by the simple-minded savage or the poet or prophet of antiquity. Some facts are almost universally known and have been the theme of comment in all ages and all lands. The Hawk that stretches her wings towards the south is as familiar to the latest Nile-boat traveller or dweller on the Bosphorus as of old to the author of the book of Job. The autumnal thronging of myriads of Waterfowl by the rivers of Asia is witnessed by the modern sportsman as it was of old by Homer. Anacreon welcomed the returning Swallow in numbers which his imitators of the colder north, to whom the associations connected with it are doubly strong, have tried in vain to excel. The Indian of the Fur-countries, in forming his rude calendar, names the recurring moons after the birds-of-passage whose arrival is coincident with their changes. But there is no need to multiply instances. The flow and ebb of the feathered tide has been sung by poets and discussed by philosophers, has given rise to proverbs and entered into popular superstitions, and yet we must say of it still that our 'ignorance is immense.' "

ALFRED NEWTON, *Dictionary of Birds*, 1896.

CHAPTER XVI

A STATEMENT OF THE MAIN PROBLEMS OF BIRD-MIGRATION

" Doth the hawk fly by thy wisdom and stretch her wings toward the south ? "
JOB, xxxix, 26.

Migration assumed to be the expression of an inborn racial custom, not the result of intelligent behaviour or of the compulsion of recurring external forces—First problem : The ends served by migration—Second problem : The ultimate cause or origin of the racial custom—Third problem : The nature of the immediate stimuli acting on the individual which bring the custom periodically into play—Fourth problem : the *modus operandi* of the custom—Summary of the argument.

IN the first part of this book an outline of the principal known facts of bird-migration was given, and in the second some special studies of the subject were made by way of more detailed illustration. In this concluding part it is proposed to discuss the main problems of theoretical interest which the facts present, and in this opening chapter the broad lines of the argument which is to be followed will be stated in brief form.

That the phenomena of migration call for explanation of a kind which science may at least attempt to provide will probably be admitted by all who can see in the natural order of things more than arbitrary arrangements of Providence : " There are occasions and causes, why and wherefore in all things." To the biologist the known facts certainly present problems of purposiveness, of causation, and of mechanism. What ends does migration serve ; what causes operate to secure the fulfilment of those ends ; and by what means do the effects of these causes find expression in the particular form in which they are known to us ?

The fundamental assumption

Before an attempt is made to see what is involved in questions of the kind which has been indicated, however, it is desirable to formulate some opinion as to the general nature of the phenomena for which explanation has to be

sought. There seem to be three conceivable alternatives: (*a*) Migration might be the result simply of intelligent action on the part of the birds and, therefore, strictly analogous to the behaviour of a human being who decides to spend his winter in a milder climate; (*b*) Migration might be the direct effect of recurrent physical forces, the migrants themselves being almost passive agents submitting to compulsion; (*c*) Migration might be the expression of an inborn racial custom, transmitted by inheritance.

The first alternative does not seem to deserve very serious consideration, for it postulates a degree of intelligence, with analytical appreciation of the recurrence of seasonal events and power of rational action, that is altogether beyond anything which one has reason to consider as characteristic of birds. The idea may safely be dismissed as an anthropomorphic fallacy.

The second alternative is also to be excluded, and for this reasons may be briefly given. Migration is far too complex and far too regular a series of events to be thought of as created anew each year by the mere pressure of external conditions. Nor are these conditions in any way adequate as causes: a bird which migrates southwards in July cannot be said to be compelled by winter to quit its northern area, and a bird which migrates from Northern Europe right across the Tropics to South Africa is doing more than would be necessary merely to avoid the rigours of the northern winter. The compulsion of external conditions may perhaps partly explain the late "weather movements" observed in severe winters, and perhaps some other movements of an irregular nature, but it is wholly inadequate as the sole cause of the regular movements of typical migration.

About true migration there is no show of reluctance: autumn departure is not postponed until the summer area has become difficult of habitation. On the contrary, the urge to migrate is so strong that even the parental instinct is overcome and late broods are often abandoned to perish in their nests. While summer is still at its height many species have felt and obeyed the impulse. The details of migration differ between one species and another, but in many cases it is also true to say that the autumn passage is far from being a gradual progress, undertaken step by step as conditions become gradually worse: it is often a speedy passage in which there is no lingering. And in some cases the journey is prolonged far beyond what mere necessity might impose. The need for departure is, indeed

anticipated, and if potential compelling forces exist their compulsion is not awaited.

Ruling out intelligent, reasoned behaviour as a sufficient causal explanation, therefore, and excluding also the possibility that migration is explained by the mere compulsion of external forces, one is left with the remaining alternative that the behaviour of migrants is the expression of an inborn racial custom which is transmitted by inheritance. Admitting, of course, that the nature of an inborn custom and of its inheritance is itself an unsolved riddle, one may proceed on the assumption that one is dealing with a racial custom of this kind, and the further implications of this view may accordingly now be examined.

One important reservation, however, must first be made, and that is that the problems are not necessarily identical for all birds in their nature and in their possible solutions. Each species and sub-species or geographical race which exhibits the migration custom differs in the nature and degree of its performance : to some extent this is true even of different communities belonging to the same morphological race. Different results may be due to different causes, and even similar results may have been brought about in different ways. The operating factors may thus vary from one case to another, and this possible source of fallacy must accordingly be constantly borne in mind in any general consideration of the subject such as is attempted here.

(A note may here be made on the use of the term " racial custom." The word " habit " is reserved by students of animal behaviour, such as Lloyd Morgan, for a routine established in the individual lifetime by dint of repetition. Such expressions as " inherited habit " and " racial habit " are accordingly contradictions in terms. Therefore, to avoid the misuse of a technical term, J. Arthur Thomson has here been followed in the employment of the non-committal word " custom " : admittedly this has a sub-audition of traditional transmission when applied to human races, but there seems to be no reason why it should not be used zoologically in a general sense without begging any questions.)

First problem

If migration is a racial custom it is certainly an expensive one, involving a great output of energy and a heavy loss of life. It follows that the custom must serve a useful end, that the cost must be more than set off by compensating

advantages, for otherwise migration would surely have ceased to exist: the stationary individuals and species would have survived and the migrants would have died out. The custom must have a *raison d'être*, and that is the first problem to be propounded, and probably the only one to which any very definite solution can be confidently offered.

In a general way the ends served by migration are indeed obvious. It enables the migrants to inhabit two different areas at the respective seasons most favourable in each. On the one hand it enables the birds native to high latitudes to escape the severity of the winter there: on the other it enables birds to exploit summer areas which in winter are unsuited to their requirements. In the next chapter, however, the factors in the seasonal changes which are of importance in this alternation of habitats will be more fully considered.

Second and third problems

The fact that there may be good reason for migration does not, of course, in itself account for the existence of the custom, although the existence of useful ends may give it a "survival value." A thing does not happen merely because it is advantageous that it should happen: some cause must operate so that the end may be attained. Moreover, in the case of an inborn custom, periodically coming into operation, the question of causation assumes a dual aspect: what originated and developed the custom in the race, and what evokes its periodical manifestations in the individual? The questions are quite distinct. The hereditary factor may be likened to the explosive power lying dormant in a cartridge: on the one hand there is the originating agent which made and packed the powder but has now ceased to operate, and on the other the stimulating agent which will pull the trigger of the gun and summon the pent-up forces into active being.

The second problem is therefore the nature of the originating cause which established the migration custom in the race, and the third problem is the nature of the immediate stimuli acting on the individual which bring the custom into operation each autumn and spring. The solution of the one must be sought in the past history of the species of birds which are concerned, and only speculation is possible: but it is not implied that the factors which were effective at some distant date were necessarily of a kind not still in

existence. The solution of the other may be sought either in the cycle of the seasons or in the physiological cycle of the bird's own life, or in both. The stimulating agent need not necessarily be a strong one, for a small movement may release a powerful spring or a gentle pressure of the trigger result in a bullet travelling for a mile : seasonal changes, as has been noted, are insufficient in themselves to cause migration, but it does not follow that they are inadequate as releasing agents for forces already pent-up and but awaiting a touch to make them active.

Much that has been written on the causation of migration is vitiated by a failure to distinguish with any clearness between the different issues involved. To confuse the ends of migration with its causes may seem an elementary error, but it has none the less been frequently made : it is said, for instance, that birds migrate to avoid the cold of winter, and this is then taken to mean that the cold of winter causes migration—an obvious *non sequitur*. A more subtle fallacy arises from the confusion of the origin or ultimate cause with the immediate stimulus or occasional cause : it is apt to be assumed, that the annual stimulus must necessarily be of the same nature as the originating cause, and that, for instance, if scarcity of food is shown not to be the annual stimulus to migration it equally cannot have played a part in originating the custom. It is, indeed, not improbable that a further subdivision should be made, and that there may be stimuli of two kinds, one preparatory and the other effective, but of this more will be said in the chapter specially devoted to what is here called the third problem.

Fourth problem

The three problems already stated do not exhaust the matter. Even were there answers to them all, there would still remain the question as to how migration, whatever its ends or causes, accomplishes its object when once the custom has been brought into play. What is the nature of the vital organisation and how does it work ? Assuming that useful ends justify the existence of migration, that sufficient causes originally brought the racial custom into being, that adequate stimuli make it operative twice a year —granted all these (although they be in truth largely mysteries) they do not in the least explain the *modus operandi*. The essence of this final problem may be expressed in two concrete questions ; " How do migrants find their way ? "

and, striking deeper still, "What determines the way to be found?" That is the final problem.

Summary of the argument

Bird-migration, then, is the expression of an inborn custom—an example of behaviour for which the capacity is inherited. It is an expensive custom and would not survive did it not serve some useful ends: the advantages of the custom, however, are in part obvious. But that useful ends are served by it does not explain the existence of migration: the presence of advantages is not in itself a causative force. The ultimate cause and origin of the racial custom must be sought in the past history of migratory species. Immediate factors, in addition to the existence of the inherited tendency, must also act as recurrent stimuli, bringing the custom into play in the individual at the proper times. Granted a useful end, an originating cause and a releasing stimulus, the *modus operandi* of migration still remains unexplained.

The problems to be considered accordingly involve several series of possible factors which may be logically grouped as follows: (a) Factors which, without being truly causative, may make migration advantageous and thus give the custom a survival value; (b) Factors which may in the past have helped to originate and develop the custom in the race; (c) Factors which periodically stimulate the custom to active expression in the individual at the proper season, to which may perhaps be added factors which may act as secondary stimuli determining the exact time of departure, whether from the winter or summer area or from some intermediate stopping place; and (d) Factors which determine the manner in which migration is actually performed. To the problems presented by each of these sets of factors separate chapters will now be devoted.

CHAPTER XVII

THE ENDS SERVED BY MIGRATION

" When by their sev'ral chiefs the troops were rang'd
With noise and clamour, as a flight of birds,
The men of Troy advanc'd ; as when the cranes,
Flying the wintry storms, send forth on high
Their dissonant clamours, while o'er th' ocean stream
They steer their course, and on their pinions bear
Battle and death to the Pygmæan race."

HOMER, " Iliad, III "
(Trans. Edward, Earl of Derby, 1864).

The general *raison d'être* of the migration habit—Winter aspects : the nature of the advantage gained by absence from high latitudes in winter—Cold and storm—Shortened daylight—Diminished food supply—Birds of different feeding habit compared—Summer aspects : the nature of the advantage gained by the return to high latitudes for the summer—Climate—Space and freedom—Lengthened daylight—Food supply—The special advantage of prolonged migration —Migration in the Tropics—Summary.

IN the foregoing general statement of the problems of bird-migration it was assumed that so expensive a custom must necessarily be of advantage to the species which possess it. This will probably be generally admitted, and indeed the *raison d'être* appears to be obvious to some extent. In general terms this consists of the exploitation of the summer opportunities of high latitudes and of the avoidance of their winter rigours : two areas are inhabited during the respective seasons most favourable in each.

It cannot, nevertheless, be dogmatically stated that the winter area or the summer area of every species is unsuited to its requirements at the other seasons of the year. Some individuals may survive the winter in what are only summer quarters for most of the other birds of the same species. Again, some species have a wide breeding range, showing extremes of climate as between one part and another : some individuals may then be resident in a part which serves others only as a winter area. It is accordingly necessary in many cases to think of the area which is in whole or part deserted at one season as being then less favourable rather than wholly unsuitable.

With this reservation one may proceed to a more detailed examination of the ends served by migration, while remembering at the same time that these do not directly explain the causes or *modus operandi* of the custom, although they may give it a survival value in the struggle for existence

Winter aspects

The advantage gained by absence from high latitudes during the winter season there is readily apparent in a general sense, but one must enquire more precisely into the nature of this advantage, or, in other words, into the nature of the circumstances which in particular make winter a season to be avoided at so great a cost and by so elaborate a means.

The primary factors to be considered are the low temperature and other meteorological conditions of winter in high latitudes, and the shortened period or even entire absence of daylight at that season. The direct importance of meteorological conditions is probably less than one would at first sight be inclined to suppose. Birds in general may be said to have considerable powers of withstanding cold. Rowan, for instance, records that he kept Juncos (*Junco hyemalis*) out of doors in open aviaries during the severe winter weather experienced in Alberta, Canada. The birds were supplied with food and proved able to withstand long periods during which the temperature scarcely rose above zero Fahrenheit and at times dropped as low as –52°F. (eighty-four degrees of frost) : this in spite of the fact that the species is naturally only a summer visitor to these parts, and that wild birds of resident species were at the same time perishing in large numbers. Rowan noted that the birds, although healthy, were easily fatigued, a circumstance which might well militate against the search for food under natural conditions. During a blizzard, also, they became incapable of perching owing to a casing of ice on the feet, and although this did no permanent damage it would be a source of danger to birds not in captivity.

Further, it has just been remarked above that many species live in high latitudes throughout the year, and in other cases some individuals successfully remain in regions from which most others of their species are at that time absent. Such individuals, however, must be subject to greater danger from occasional accentuations of the conditions beyond the extreme which can be tolerated, as when

an exceptional frost levies a heavy toll. In this country an unusually hard winter causes great destruction of bird life, and particulars of this, in the case of the winter 1916–17, have been recorded by Jourdain and Witherby.

It is possible that the lessened or absent daylight is of direct importance, but definite evidence is lacking.

It is thus probably to the secondary factors that one must chiefly look, namely, the effects of winter upon food supply. For a great many species of birds the scarcity of insect life in winter practically means the disappearance of their accustomed food, and in a lesser degree the supply of various other forms of food for different birds is diminished. Again, the freezing of both land and water, and the mantle of snow on the ground, make the food of many species of birds inaccessible. The shortened hours of daylight contribute in a different way to produce the same effect, for the daily period during which feeding can take place is thus greatly decreased, a point of importance considering the length of time which is in so many cases requisite for the obtaining of an adequate meal: it must be remembered, however, that there are migratory birds which are wholly or partially nocturnal in their feeding habits.

That it is the effect on food supply which is most important is an argument for which evidence may be obtained from a consideration of the incidence of migration among species of different feeding habits. It is, for instance, among insectivorous species that migration is most generally and most notably developed. In this group none passes the winter in very high latitudes and only a few species remain even in temperate regions, and the period of absence is usually a long one.

Next in order of importance as migrants may be placed the eaters of seeds and fruits. These find an abundant supply of food in the autumn, and this lasts until either the supply itself approaches exhaustion or deep snow or shortened daylight handicaps the search. Birds of this group are on the whole later in their departure from high latitudes and undertake shorter journeys than the insectivorous species.

Birds of other habits are affected in different degrees. Marsh and water fowl are probably affected chiefly by the freezing of their feeding places. Birds of prey are affected in a secondary way through the departure of the small birds and the hibernation of the small mammals upon which they feed. The least affected of all are the sea birds, which con-

tinue to find their food except in those highest latitudes in which the sea itself is frozen. It is among the sea-fowl that one finds many of the species which remain in high latitudes throughout the year.

These generalisations must not, however, be pressed too far, for many exceptions could be quoted. To give a single instance, the fish-eating Terns are among the most notable of migratory birds. There seems to be some ground, nevertheless, for the conclusion that the feeding habits of a species constitute an important factor, and that one of the chief ends served by absence from high latitudes in winter is therefore the safeguarding of the food supply. To say this does not, of course, necessarily imply that cold and darkness are of no direct importance.

Summer aspects

What are the advantages of return to high latitudes for the summer ? Why, in other words, might not those birds which are unsuited to permanent residence in high latitudes remain always in their winter quarters ? To say that the heat, glare, and (in some cases) drought of summer in low latitudes is not readily tolerated by birds native to temperate or polar countries is no answer, or at best only a partial one. Many of these birds spend their winter in parts of the Tropics where the conditions are relatively constant. That birds may suffer distress from excessive heat may be admitted, but in very many cases this factor seems to have little possible relation to the circumstances.

It seems probable that it is for the purposes of the breeding season that the summer in high latitudes is particularly advantageous, and that the lower latitudes which serve during the non-reproductive season are unsuited to the more arduous life of the adults in summer and to the early days of the young birds. The mere question of climate may certainly come in here, but there are secondary factors which seem likely to be more important.

For the breeding season there are many special requirements, the chief of which are the sufficiency and suitability of nesting sites, safety from enemies, and an abundant food supply both for the busy parents and for the growing young. More elbow-room, so to speak, may be an advantage —wider feeding and breeding grounds, greater choice of nesting sites, and more freedom from overcrowding, competition, and danger. In other words, an area which may seem

suitable for the individual bird may provide favourable conditions for only a limited population: the fact that in many cases each pair of breeding birds requires a distinct territory of its own, vigorously denied to other birds of the same species or of other competitive species, has been specially stressed by Howard with regard to migration. An abundance of food, readily procurable, must be highly important; and here, too, the long daylight of the summer in high latitudes will play a part, giving more time for the ceaseless labours of nesting and for the search for food for many mouths.

With regard to this last point it has recently been stated by English that resident tropical birds with nidicolous young (*i.e.* fed by the parents) tend to have smaller broods than species which nest in high latitudes. There is some evidence, indeed, that in the case of a single species larger clutches may be laid in the higher latitudes than in the lower latitudes of its breeding range. If this may be taken as related to the length of day available for the search for food, it indicates an advantage in spring migration from the Tropics to high latitudes which would not be served by, say, finding a temperate climate closer at hand at a suitable level on some tropical mountain range.

It would seem that if there were not migration there could be but relatively few birds in high latitudes, and those restricted to such manners of life as are possible there all the year round. If that were so the great opportunities of the summer of extreme northern and southern regions would pass almost unexploited, and there would be what has been not inaptly called a "zoological vacuum." In the ceaseless struggle for existence, however, opportunities are always used, and it is not surprising that in the course of evolution the potential vacuum has been filled. But it is only through the existence of the migration custom that birds are enabled to make full use of the space, and of the daylight and the food, which are available in summer in those latitudes where the winter conditions do not permit the permanent residence of more than a few species specially adapted thereto.

Special advantages of trans-equatorial migration

It is perhaps as regards length of daylight that there is advantage in what would otherwise seem to be an unnecessarily long journey into the temperate region of the opposite hemisphere. Migrants which go so far keep per-

petual summer and the long daylight hours found in high latitudes at that season : so they gain an advantage which would not accrue in merely the mild winter of the lower latitudes of their native hemisphere.

Special conditions relative to migration in the Tropics

One usually thinks of migration as it is typically found in birds which breed in temperate or subarctic regions, and fhe foregoing discussion has been mainly from that point to view. There is, however, migration of a kind among birds which never leave the Tropics. There are many stationary tropical birds, and there are probably parts of the tropical regions of the world in which the native birds all tend to be non-migratory. In some tropical regions there are notable seasonal movements which apparently must be classed as definite migrations even although the distances covered are possibly not very great. Information on the subject is extremely scanty, but it is obvious that the considerations already discussed in this chapter must in some measure be inapplicable.

Lynes has recently made some important observations on this subject during a long expedition in the Darfur Province of the Sudan, lying within some fifteen degrees of the Equator. Apart from the appearances of winter visitors and birds of passage of Palæarctic species, he found evidence of definite seasonal movements on the part of purely African birds. In the season of the annual rains, occurring at the time which is summer in higher latitudes, many species come up from the south to breed in Darfur, or pass through to breed rather more to the north. At or about the same time other species come up from the south to spend their off-season in or north of Darfur, having bred farther south during the other part of the year.

The relevant environmental circumstance is here no doubt the alternation of a wet and a dry season. It is suggested that the southward migration of the northerly breeding birds serves the purpose of avoiding the season of drought in their native area. On the other hand, the southerly breeding birds avoid, in their off-season, the heavy rains in the equatorial forests, with their choking growth of vegetation and excessive wetness at that time. Here again it is probably not climatic conditions directly, but the effects of climate upon food supply, which are important.

Lynes remarks that as a bird-habitat the Sudanese arid

belt—this open region of annual rains lying south of the permanent desert, and north of the savana country and of the equatorial forests beyond it—" may well be likened to the Arctic regions : both are in summer well suited to the requirements of a varied and a breeding-bird population ; both are in winter unsuitable, because there is not enough food ; in the Arctic through ice, snow, and darkness, and in the arid belt through drought." At the same time it must be noted that the arid belt in the dry season meets the needs of many birds, both Palæarctic migrants and native residents, the latter including some which breed at that time of year : this in spite of the fact that in wide areas no water is then available for drinking, even in the form of dew.

The conclusion to be drawn from the discussion in this chapter would seem to be that although the general nature of the ends served by the migration custom may be obvious, there remains room for further speculation and inquiry as to the relative importance of the different factors which may be involved.

SUMMARY

Migration is an expensive custom which must be assumed to serve ends which are of advantage to the species exhibiting it. The advantage, in general terms, is obviously that it enables birds to inhabit two different regions during the seasons respectively most favourable in each : the summer opportunities of high latitudes can be exploited, while their winter rigours can be avoided. In more detail, the nature of this advantage appears to involve several factors. The advantage of absence in winter from high latitudes lies in the avoidance of the cold and stormy weather, in the avoidance of the short hours of daylight available for the search for food, and in the avoidance of the effects of these primary conditions upon the abundance and accessibility of the food supply. The advantage of return to these latitudes for the summer lies in the availability of suitable breeding places, in the existence of long hours of daylight for the search for food when most food is required, and in the abundance at the same time of the food supply itself—a supply which without migration could be but little utilised by any birds. The special advantage of migration which takes place not merely from high latitudes to low latitudes but from high northern latitudes to high southern latitudes, probably lies chiefly in the long hours of daylight which are thus found

throughout a year of perpetual summer. Birds which are migratory wholly within the Tropics are subject to special conditions, of which the effects of alternate wet and dry seasons upon the food-supply in different types of country are possibly the most important.

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CHAPTER XVIII

THE ORIGINATING CAUSE OF THE MIGRATION CUSTOM

" O swallow, sister, O fair swift swallow,
Why wilt thou fly after spring to the south
The soft south whither thy heart is set ? "

SWINBURNE, " Itylus."

The serving of ends does not explain causation—Migration assumed to be a racial custom—Only speculation possible as to the origin of the custom—Theories involve some great compelling cause in the past history of migratory species—Great climatic changes a possible cause : the glacial epoch theory—Alternative theory based on assumed spread from an original area of resident habitation—Synoptic view of the theories—The custom possibly a thing of sudden growth : the case of Pallas's Sandgrouse—Difficulties and complexities in theories on the subject—Theories of causation do not explain the nature of a racial custom nor the manner of its inheritance.

IN the previous chapter the ends served by the existence of the racial custom of migration were discussed, but the distinction between ends and causes has been carefully preserved. That the custom has advantages is no explanation of its origin, although it may be an explanation of its survival. Nor can one imagine that the factors which make migration advantageous would be sufficient to cause it by the mere compulsion of their external force, even if one could think of migration as created anew each season in this way.

Everything points to the conclusion that migration is a custom which forms part of the inheritance of the species and which is evoked to repeated activity by periodically recurring stimuli. For the origin of such an inborn custom one must obviously look to the past history of the races of migratory birds, and in this field no more than speculation is possible. The question of the evoking stimuli, acting on the individual as the seasons recur, may be left for a subsequent chapter : this one will be confined to the question of the originating cause of the racial custom.

All evolutionary theories of the origin of migration necessarily assume that the performance of migration by individual birds to-day is the result, and to a greater or less

extent a customary repetition, of an event or series of events in their racial history. Just as the individual organism in the course of its structural development often recapitulates stages of the evolution of the type, so the migrations now performed by the individual bird may reproduce features of some great movement in the history of its race.

The theories which it is possible to state on this general basis vary according to the nature of the factors supposed to have been concerned, and according to the initial assumptions which are made as to the distribution of now migratory species, or of their ancestors, in the pre-migratory stage. Broadly speaking, there are two main types of theory: the one relies on the supposed influence of great physical changes, geological and climatic, upon the conditions of life upon the face of the earth; the other seeks a purely biological explanation. As to pre-migratory distribution, various assumptions can in either case be made: a wide permanent distribution can be supposed to have become subsequently restricted according to season, or a limited permanent area can be supposed to have become a centre for such temporary dispersal as the seasons permit: either the present summer quarters, the present winter quarters, or some now new neutral area, can be theoretically taken as the original home.

Theories based on great physical changes

One of the possible views was expressed by Wallace in a passage which has become classical to students of the subject and which may once more be quoted here. "It appears to me probable," he wrote, "that here, as in many other cases, 'survival of the fittest' will be found to have had a powerful influence. Let us suppose that in any species of migratory bird, breeding can, as a rule, be safely accomplished in a given area; and further, that during a great part of the rest of the year sufficient food cannot be obtained in that area. It will follow that those birds which do not leave the breeding area at the proper season will suffer, and ultimately become extinct; which will also be the fate of those which do not leave the feeding area at the proper time. Now, if we suppose that the two areas were (for some remote ancestor of the existing species) coincident, but by geological and climatic changes gradually diverged from each other, we can easily understand how the habit of incipient and partial migration at the proper seasons would at last become hereditary, and so fixed as to be what we

term an instinct. It will probably be found that every gradation still exists in various parts of the world, from a complete coincidence to a complete separation of the breeding and subsistence areas; and when the natural history of a sufficient number of species in all parts of the world is thoroughly worked out, we may find every link between species which never leave a restricted area in which they breed and live the whole year round, to those other cases in which the two areas are absolutely separated." The prediction made in the final sentence of this passage, it may be added, has since been fulfilled.

This theory recognises the two seasonal phases in the annual cycle of the bird's life—the reproductive phase and the winter feeding phase—each with its own special requirements. The areas in which the two sets of requirements were met are supposed to have been originally coincident, as in the case of wholly stationary species to-day, but to have gradually diverged as the geological and climatic conditions slowly changed. One can thus imagine, for example, a species as resident in high latitudes during a period of mild climatic conditions and acquiring, as the climate became more severe, a winter feeding area which gradually moved towards lower latitudes, at first overlapping the breeding area, then lying adjacent to it, and finally separated from it by an intervening tract unsuited to either phase of life. Other examples of the possible working of the same principle can be thought out, according to the assumptions made as to initial distribution and as to the nature of the external changes.

The hypothesis is perhaps not completely satisfying. It by no means explains everything, and the attempt to apply it in detail raises various difficulties. Yet as a general statement of a theory of this type it cannot easily be improved upon even in the light of the fuller knowledge of the facts of present-day migration which are now available.

It is indeed doubtful whether it is profitable to attempt to frame any more definite theory on these lines. It is, of course, well known that in past geological ages, and going no further back than those which have occurred within the period that birds have existed, there have been both great changes in the distribution of land and water on the earth's surface and great climatic changes. The data of palæogeography and palæoclimatology do provide some material for the ingenious ornithological theorist, but the gaps are very great and there is little chance of verifying

any detailed hypothesis. For present purposes, therefore, it will suffice to mention one particular theory of the kind.

Various authors, such as Weismann, Tristram, Seebohm, and Dixon, have invoked the Glacial Epoch—the "Great Ice Age" of Pleistocene times—as one of the chief factors influencing distribution in such a way as to give rise to the migration custom. The idea has taken different forms, but a typical theory assumes that before the glacial epoch birds were non-migratory, and that species which are now only summer visitors to high northern latitudes were then resident there. (Deichler and others have quoted the palæontological evidence favouring the view that some species had a wide distribution in pre-glacial times.) The polar ice-cap crept downwards as the epoch dawned and pressed the bird population before it, until eventually bird life was concentrated in low latitudes. Ages passed and the ice-cap receded. Each spring the birds formerly driven from the north now strove towards the old home of their race, but each autumn they withdrew to the second home to which their intermediate ancestors had become accustomed. As the ice-cap shrank the journeys performed twice a year became longer and longer until at last the climatic conditions of the present became established and with them bird-migration as it is known to-day. The individual migrants follow the path of a great racial movement of the dim past. Such is the imagined history. In an attempt to explain complications for which the theory seems insufficient, it has sometimes been assumed that not one glacial period but a sequence of two or three must have played a part. Into these elaborations it is not necessary to enter here, for the available knowledge of the case does not warrant speculation on anything but the broadest of general lines.

Schenk (1924), among others, has criticised this theory on the ground that the facts of migration at the present time do not show the necessary correspondence with what is known to geologists of the distribution of glaciation in the ice-age. Although it is not here desired specially to support the theory, it may be pointed out that the objection applies strongly only to the cruder forms of the idea. For one thing, it is not only the mere extent of actual glaciation that must be taken into account, but also the whole of the effect upon the climate of a much wider region. In the second place, allowance has to be made for subsequent

modification under the influence of other factors which have been operative in the intervening period. It is not at all necessary that one should assume that the areas of seasonal habitation and the paths of migration movement have undergone no subsequent evolution.

A simpler form of the glacial epoch theory begins with the turning-point in time at which the ice-cap may be supposed to have begun to shrink. A concentration of bird life in low latitudes at this stage is assumed as before, and a gradual northward extension of summer range, kept in waning check by the receding ice, is supposed to have occurred. In this less ambitious attempt at a theory the idea of an instinct to return to the supposed pre-glacial homes in high latitudes is wanting, and the recession of the ice-cap represents no more than the removal of a check on a supposed natural tendency towards expansion of range. It is, however, difficult in any event to believe that an instinctive longing for these ancient areas would have survived the age-long period of residence in low latitudes while the ice-cap held all attempts at migration in abeyance. It seems easier to suppose that the instinct to return to one area or the other was only kept alive by some annual movement between the two from the very beginning, and for this reason the earlier stage in the more elaborate theory seems to be rather far-fetched.

Theories based on range expansion from biological causes

In opposition to the theories which lay stress on great climatic changes in the past, the view put forward by Brooks may be quoted, as follows: "While most writers on the subject have thought that migration had its origin in an annual journey which, while short, was definite for all the members of the species, and while they have felt forced to call in the aid of geology to account for the gradual separation of the two termini, and the length of the journey from one to the other, the hypothesis of geological change seems gratuitous and unnecessary, since the known habits and instincts and needs of the birds are, in themselves, a sufficient explanation of all the broader and more general characteristics of migration. It seems much more simple, and much more consistent with our knowledge of the past history of living things in general, to believe it had its origin in an intense but geographically indefinite impulse,

which led birds to scatter at the breeding seasons, and to hunt out safe hiding places for their nests, and that, as enemies also improved in power to find the most accessible nests, the instinct gradually shaped itself into definiteness through selection and extermination, until, at last, safe breeding grounds far away from home and far away from the enemies which there abounded, have become established, and until many species have come to share the impulse to resort to these selected breeding places on the approach of the period of sexual excitement, and to follow the same path between points far apart; that the increasing safety of the eggs and young has permitted a low birth-rate, and the improvement by selection of the power of rapid and long-continued flight; and that this has, in its turn, permitted migration to become longer and longer, and more and more protective to the eggs and young." This view, it will be seen, accounts for the origin of migration by assuming a process of evolution governed by purely biological factors, which include the competitive interactions of different species, and which are independent of any great physical changes affecting the conditions of life during the history of the race. The special factor supposed to have been at work in producing the original overflow from the area of stationary habitation is the quest for breeding places, and the assumption is implied that the winter quarters rather than the present breeding range represent the primary home of the species. On this theory, therefore, migratory species of birds have in very many cases given up breeding in their original area, and the rather strange assumption seems to be implied that each species began by inhabiting an area which was, or inevitably became, less well suited to its breeding requirements than some distant land of promise.

It would seem more reasonable to suppose that the original area was not unsuited to the requirements of the birds, but that it became inadequate as they multiplied. Overpopulation might then have led to the dispersal of the surplus birds in the manner suggested. Some other factor would then have to be invoked to account for the eventual complete abandonment of the original home as a breeding area, and the departure of even those birds which it was in the first place able to accommodate. Here, perhaps, there is scope for a complex theory combining some such process as that suggested by Brooks with the intercurrent or subsequent action of geological or climatic changes.

A view put forward by Howard resembles that of Brooks in being based on range expansion due to the search for places suitable for breeding. Here, however, special stress is laid upon the tendency of each pair to acquire and defend, to the exclusion of others, a particular and sufficient territory of its own during the breeding season: in birds which breed in communities this territory may be no more than space for the egg or eggs, or for the nest if there be one, but in other cases it is also an exclusive feeding ground for the time being and may be of considerable or even large extent. This territorial tendency puts a limit upon the population which any area can support, and in the case of an increasing species this would lead to range expansion, eventually encroaching on regions unsuitable for habitation except in summer.

Howard's exposition has the special merit of including an explanation of the return movement which is quite in line with the first part of his theory. Just as the instinct of exclusiveness led to dispersion for the breeding season, so would the supervening instinct of gregariousness lead to concentration when that season had passed. Flocks would be formed to spend the winter in search of food, and the ones which would most readily survive would be those which showed a tendency to return in the direction from which expansion took place and thus most certainly to find hospitable conditions.

Not altogether dissimilar to the views of Brooks and of Howard is the kind of theory favoured by such writers as Braun, Taverner, and Pycraft. In it, however, the reason for original dispersal is assumed to be the quest for food, especially for food in the breeding season, rather than for nesting-sites or breeding territories. It is pointed out by Pycraft, for instance, that a resident species is wholly restricted to the area in which its food would be available all the year round, and that this area can support only a limited number of birds: it follows that resident species tend to be individually less numerous than their migratory relatives. It is supposed, accordingly, that migration has resulted from the overflow of certain increasing and adaptable species from the area in which their food was available throughout the year. "Composed of individuals subsisting on a food of universal range, but limited in supply they were enabled to roam farther afield as their numbers strained this supply in their immediate neighbourhood. Annually, however, a check was placed on further extensions of range

by the cares of breeding and by the diminution of food at the end of the breeding season—whether caused by the climate or otherwise—while behind them the supply was increasing. Thus they were drawn back towards their starting-point. Again threatened by famine, they once more turned outwards, finding the earlier depleted area restocked. These movements, in short, were doubtless then, as now, periodic, and determined largely, if not entirely, by seasonal changes."

In this form, and without further elaboration, the food quest theory does not seem wholly to cover the case of species which have nowhere any area of resident habitation but alternate between two regions, one of which is solely a breeding area and the other solely a winter area. Which of these two areas, if indeed either, is to be considered as the original home of the species or of its ancestors in the pre-migratory stage ?

Eckardt supports the view that expansion of range in quest of space and of food was the originating factor, but he attaches special importance to the long daylight found in high latitudes during part of the year. He argues that this would have been significant even in the pre-glacial period when there was a uniform tropical climate in Europe. Seebohm, an exponent of the glacial epoch theory, also thought that the daylight factor had probably led to there being some degree of migration in pre-glacial times.

A synoptic view of the theories

A useful analysis of the views of earlier writers on this and kindred questions was presented by Herman, a Hungarian authority, to the British Ornithologists' Union on the occasion of the International Ornithological Congress held in London twenty years ago. In the present work, however, no attempt has been made to repeat or continue that task, or to give an historical account of the various theories, or to present fully the views of particular writers. The references given at the end of the chapter include some noteworthy contributions, not all of them specially mentioned in the text, which have helped towards building up the general body of theory as it exists to-day. Of this, as it appears to the writer, some general account may now be given, as a supplement to the statements of particular theories which have just been made.

It may be generally admitted that migratory birds have

evolved from a non-migratory stock, because obviously migration in high degree has been possible only since the acquisition of good powers of flight. The various theories accordingly agree in assuming a gradual evolution of a racial custom of seasonal migration, and thus a progressive differentiation between summer and winter areas. The particular theories which have just been outlined are representative of the many speculative views which have been expressed, and they seem to typify three main possible lines of explanation. These may accordingly now be stated in their most general terms in order that a clearer view may be obtained of the possible answers to the question with which this chapter is concerned.

(A) The original distribution of a given species (or its prototype) in the pre-migratory stage may have roughly coincided with, or have included, the present summer area in high latitudes. The onset of severer climatic conditions than those formerly enjoyed, and possibly than those now prevailing, may have made the whole or a part of this area unsuitable for winter habitation. Migration may thus have become imposed as a necessity upon the birds, subsequently developing into a perfected racial custom by virtue of which annual performance came to precede the recurring necessity, and retaining its character although the necessity in time became somewhat less. In this view the glacial epoch, if it be supposed to be the climatic change in question, did not cause complete abandonment of the area in high latitudes, but left localities which were possible for summer habitation as is the case to-day in Arctic or Alpine regions. The theory does not offer any ready explanation of the definiteness of winter areas, and other factors must be invoked to account for this as a subsequent modification.

(B) The original distribution in the pre-migratory stage may have roughly coincided with, or have included, the present summer area in high latitudes, as before. But this may have been followed by a period when high latitudes had to be altogether abandoned owing to glaciation, and when the birds consequently gradually concentrated, still as residents, in low latitudes. This would be followed by the recession of the ice-cap and the concurrent resettlement, this time on a summer-visitant basis, of the original area for which the birds are supposed to have retained some inherited longing.

(C) The original distribution in the pre-migratory stage

may have been in the present winter area or in some other and now neutral region in low latitudes. From there gradual expansion into higher latitudes, on a summer-visitant basis, may have taken place as the result of over-population in the original area and the need for fresh sources of food and wider breeding grounds. (If this expansion be supposed to have followed the wane of a glacial epoch, the latter was no more than an incidental limiting factor.) The gap in this kind of theory is the absence of an explanation for the complete abandonment as a breeding region, in many cases, of the supposed original area : other factors making this unsuitable for reproductive life must therefore be imagined as coming subsequently into operation.

It will be observed that the first and third theories are diametrically opposed as regards the initial assumption which is made as to the original area of resident habitation : the second, by an elaboration, almost combines the two alternatives. In the first theory, the originating force is the compulsion of physical changes in the environment. In the second it is the inherited longing for an ancestral area which had been lost owing to intervening physical changes. In the third it is the urge of biological factors tending towards range expansion.

Of the three, the second theory demands the most elaborate initial assumption and invokes the least credible motive force—an inherited longing for a former area surviving an age-long period of exclusion therefrom. Of the other two theories it may be said that neither offers a complete explanation unless something be attributed to the modifying action of supplementary factors. Between them it seems impossible to judge : in the absence of good evidence as to the date when migration originated, and of the distribution of now migratory birds or their prototypes before that time, it becomes largely a matter of opinion as to which type of cause is most likely to have been effective.

It therefore seems that if one wishes to formulate any definite statement as to the probable origin of migration it must needs be in very general terms. This may perhaps be attempted in a paraphrase of Wallace's words but omitting his particular view. Let it be assumed that for any species of migratory bird there is a certain area suitable for the breeding season ; and further, that there is a certain area suitable for non-reproductive life during a great part

of the rest of the year. Now let it be assumed that the two areas were once (for some remote ancestor of the existing species) coincident, but that, owing to external changes or to changes in the requirements of the species or to a combination of both kinds of change, they gradually diverged from each other. It can then be supposed that a racial custom of migration at the proper seasons would be evolved *pari passu* with this divergence of the suitable areas. This process of evolution would show every gradation from the original complete coincidence of the areas to their eventual entire separation.

Possible sudden growth of the custom

There is just one other suggestion which may here be made. Most theories of the origin of migration assume that the custom was a thing of slow growth, built up only gradually in the course of ages. These views have perhaps been coloured by the general conception of evolution as a thing taking place only by imperceptible stages through very long periods of time. In recent years, however, it has come to be recognised that even structural evolution may take place also by sudden jumps, "mutations" appearing abruptly and achieving instant success. May one not draw a parallel to this in the field of functional evolution and consider the possibility of migration having been a thing of sudden growth ?

Taverner perhaps hinted at some theory of this kind when he pointed out that migration to and from true oceanic islands —islands far from continental coasts and unconnected by land bridges at any relevant geological period—must necessarily have had an abrupt origin, intermediate stages being obviously impossible. He expressed the further opinion, however, that this could only have happened in the case of species which had already a highly developed capacity for migration, gained as the result of the evolution of migration on the continental land-masses.

In an earlier chapter some account was given of the "irruptions" of Pallas's Sandgrouse (*Syrrhaptes paradoxus*), those extraordinary movements that sometimes take place from Central Asia and reach as far as north-western Europe. It is true that one cannot explain them, but one knows that they exist : one knows that, perhaps by reason of overcrowding or other adverse conditions, this almost resident species may suddenly perform a spring migration of great

extent, that the establishment of new summer quarters may be attempted, and that there may be some hint of a return movement of survivors in the autumn. Had the new summer quarters proved more favourable, might not this species have suddenly changed from a resident to a regular migrant on any one or more of the occasions on which it has, so to speak, broken bounds ? The point is that one has here no mere gradual extension of range but an abrupt attempt to find a new and distant home. May not such occurrences as these be the beginnings, or attempted beginnings, of migration proper ? On the other hand, however, it might be argued that they are rather the last echoes of a custom which has been lost.

Difficulties and reservations

In dealing with speculations as to the origin of migration it is necessary to recognise certain difficulties lest the problem tend to assume too simple a form in one's mind. Not one cause but a complex series of causes may have operated. The problem may not be the same for all birds but be a different one in different cases. Something depends upon the date to which the origin of migration may be assigned : if one goes far enough back in geological time one will be dealing not with the species of to-day but with the stocks from which they sprang, and the present-day distribution of species may thus be of little significance. In considering present-day distribution one must also take into account the other factors which may have modified this since, and so have altered the picture which survives.

It is perhaps desirable to make the further reservation that all theories of the kind which have been considered seek only to find a sufficient originating cause. They do not attempt to explain how such a cause may operate to produce a racial custom, or how a custom so produced may be inherited. This question of the nature of inherited forms of behaviour is one which is in no way peculiar to the special problem of bird-migration, and it is not necessary to attempt to deal with it here. For present purposes it is sufficient to assume that inherited forms of behaviour do exist and can be originated by, or developed to meet, pressure of circumstances affecting the race : to consider the possible nature of these circumstances is the most that has been here attempted.

SUMMARY

The purposes served by migration do not in themselves explain its causation. Migration is assumed to be an innate racial custom, and only speculation is possible as to its origin. The various possible theories involve some great compelling cause in the past history of migratory birds, the movements thus caused afterwards becoming, by some means, customary in the race. The most general hypothesis assumes that the areas suitable respectively, in any instance, for reproductive life and for winter feeding were originally coincident, but gradually diverged, either owing to changes in the prevailing conditions or to changes in the requirements of the birds, or to a combination of both. One form of special theory seeks the origin of migration in great climatic changes such as glacial epochs ; another seeks it in the natural spread of species, in quest of new nesting sites or of fresh sources of food, from an originally restricted area of resident habitation. As an alternative to the gradual evolution of the custom, may be considered the possibility of its having been of more sudden growth, starting in any given instance with an abrupt movement such as occurs to-day in cases like that of Pallas's Sandgrouse. All theories which seek to explain the origin of migration are, however, beset with difficulties and complexities. Nor do these theories explain the nature of the inborn custom or the manner of its inheritance.

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CHAPTER XIX

THE NATURE OF THE ANNUALLY RECURRING STIMULI TO MIGRATION

" And as a stork which idle boys have trapped,
And tied him in a yard, at autumn sees
Flocks of his kind pass flying o'er his head
To warmer lands and coasts that keep the sun,
He strains to join their flight and from his shed
Follows them with a long complaining cry—
So Hermod cried, and yearned to join his kin."

MATTHEW ARNOLD, " Balder Dead."

Factors insufficient as compelling causes may act as releasing stimuli—Sources of stimulus may be external or internal—Possible external influences: climatic factors—Variations in length of daylight—Changes in food supply—Possible internal influences: physiological factors—Difficulties and complexities in the various explanations—External and internal factors not wholly separable—Unrest before migration—General conclusions: statement of a provisional combined theory—Summary.

IT has been assumed in the foregoing chapters that migration is a racial and largely hereditary custom, that it is one which serves useful ends, and one which owes its origin to some compelling cause in the past history of migratory birds. It has now to be considered what factors are concerned in the seasonal emergence of the racial custom from the ordinary behaviour of the individual bird, or, in other words, what forces act as releasing stimuli, or " occasional causes," and periodically evoke the custom to active expression.

It has already been argued that external forces such as climatic conditions are not adequate as causes of migration: that, for instance, the cold of winter cannot be considered as driving southwards a bird which migrates in July, or as driving from the northern temperate zone to the southern temperate zone a bird which would have found an almost equivalent refuge in the northern sub-tropics. It has been pointed out, however, that factors which may be inadequate as motive causes may still act as releasing stimuli. Given the inborn but latent custom of migration, engendered in the race in some such way as was discussed in the previous

chapter, it is possible to imagine very slight external forces as, so to speak, pulling the trigger which in a sense causes the explosion, but which may be more accurately described as releasing a pent-up power originated by quite other means.

This chapter is accordingly concerned with factors which do not create or compel migration, but which act merely as releasing stimuli, and it has to be remembered that very slight forces may in this case be sufficient.

There appear to be two possible sources of stimulus, external and internal. The stimulus may come from without and be some factor in the annual cycle of seasonal change in the physical world. Or the stimulus may come from within and be some factor in the annual cycle of physiological change in the organism itself.

Possible external stimuli

Among possible external stimuli, various climatic factors at once suggest themselves, especially with regard to the autumn migration. The first hint of winter cold, for instance, might be sufficient stimulus, or perhaps it should be said that a given degree of cold might in any particular case be stimulus enough : as different birds migrate at different times it is obviously necessary to assume that the stimulus required differs, at least in degree but possibly in kind, in different cases. Temperature is not the only possible climatic factor, of course, and in the chapter dealing with the relation of meteorological phenomena to migration the part which variations in barometric pressure may play has been sufficiently indicated.

Another possible factor may be found in the variations in the length of daylight throughout the year. This factor has the special attraction for the theorist that it is by far the most regular of the physical changes in the seasonal cycle, and, therefore, the one which would seem most capable of correlation with the wonderfully punctual manifestations of migration. Among writers who have favoured this idea, Eifrig has drawn attention to the analogy provided by the regular flowering of different species of plants at various times of year, and to recent botanical evidence of an experimental kind " tending to show that the length of day may exercise a remarkable regulatory action in initiating or inhibiting sexual reproduction." Argument based on analogy must, of course, be accepted with reserve,

and there are difficulties, not to be disregarded in the absence of any direct evidence, in the way of accepting any simple theory of "photoperiodism" as explaining the seasonal emergence of migration behaviour in birds.

Still another possible factor is the decrease of food supply or the increased difficulty, from one cause or another, of making use of it. Magnetic phenomena have also been suggested, but no evidence exists which seems to give any probability to such a theory.

The possible factors in spring are to some extent the reverse of those which operate in autumn, but difficulties which will presently be mentioned become apparent if one attempts to press this generalisation too far.

Possible internal stimuli

It is especially with regard to the spring migration that internal factors have been considered likely to play an important part. It has, indeed, been for long assumed that at this season migration is to some extent bound up with the advent of the breeding period, and that it is in the re-activation of the reproductive functions and instincts that the stimulus occurs to the return to the summer nesting area of the species. On this basis one may regard spring migration as the first phase of annual reproductive activity. In physiological terms, it might be said that the stimulus is to be found in some effect of the internal secretions of the enlarging sexual glands.

Similarly, it is possible to imagine that the waning of reproductive activity may in some way be the signal for the return migration in autumn.

The alternation between reproductive and non-reproductive phases is not, however, the only periodic factor in the physiology of birds. There is also the periodic moulting of plumage, partial or complete, which usually takes place once or twice a year. Where there are two moults they are in most cases in autumn and in spring, and in many cases migration seems to follow moulting. The time of moulting cannot but be a period of notable physiological stress, and the existence of an annual rhythm determining or determined by moulting is a conceivable factor to be considered, although it would seem inapplicable to some species. There is also the annual alternation between exclusiveness and gregariousness in the social behaviour of birds, which Howard has urged as specially important in regard to

migration, as has been mentioned in previous chapters : but this is itself directly linked with the reproductive cycle.

Difficulties in the way of any simple explanation : autumn migration

There are undoubtedly some serious difficulties in the way of accepting any one simple theory of the nature of the stimulus to migration. Temperature alone, for instance, will scarcely suffice as a complete explanation of the stimulus to autumn departure. The temperature figures for different years vary widely, and apparently to a much greater extent than the dates of migration movements.

There is a difficulty also in attributing the stimulating effect to such influences as the distribution of atmospheric pressure may have. It has been mentioned elsewhere that a clear relationship exists between migration movements and certain meteorological conditions at the starting-point. This cannot, however, contain more than a small part of the answer to the problem. The favourable conditions are in large measure the same in autumn and in spring, and they may occur at any time of the year. It is only at the appropriate seasons that the conditions lead to migration, and these conditions must, therefore, be regarded merely as a stimulus to the actual inception of migration flight. Until the urge to migrate has been aroused the conditions will not lead to migration : otherwise, indeed, this would occur at the most inappropriate moments, say, in the middle of the nesting season, just because the propitious combination of meteorological circumstances happened to come into being.

It is doubtful whether variations in the food supply are more uniform from year to year than the variations in climatic conditions, but the possible influence of this factor must not be overlooked. Of all the seasonal changes the most regular is the variation in the length of daylight, and some importance should possibly be attached to this factor. There is nevertheless a difficulty, long ago remarked upon by Newton, that a migrant which flies southwards from high latitudes in July or August is actually going towards a zone of shorter daylight, although one which will later on have the advantage in this respect. Similarly, a migrant leaving the Tropics before the vernal equinox flies towards an area in which, at the moment, the days are shorter. It does not seem, however, that this by any means necessarily rules out the possibility that the shortening daylight after mid-

summer may have a stimulating effect, for in this regard it is the absolute state of affairs at the starting-point that is relevant and not its relation to conditions elsewhere.

Difficulties in the way of any simple explanation : spring migration

Still greater difficulties, as has already been hinted, arise when the attempt is made to find external factors which might serve as stimuli to migration in spring. In the summer quarters of the migrants the temperature is rising, the daylight lengthening, and the food supply increasing—everything grows favourable for the return of the birds. Many of the migrants, however, are entirely removed from the influence of these factors : they are wintering in the Tropics where many of the conditions are constant, where the length of daylight does not vary, and where the cycle of the seasons as known in high latitudes plays no part. In some parts of the Tropics there is a regular cycle of wet and dry seasons, but this does not necessarily synchronise with the seasonal changes in higher latitudes.

On the other hand, an important objection to the purely physiological theory will be obvious. Mention has been made of the annual cycle of reproductive activity, but this applies only to adult birds. Young birds a few weeks old perform the autumn journey, and in those species which take two or more seasons to become mature there is also a spring migration and autumn migration of full-grown but non-breeding birds, although it seems likely that these movements are sometimes neither so complete nor so perfect as those of the adults.

Are external and internal factors separable ?

It may also be doubted whether these periodic physiological phenomena should, indeed, be considered separately from the external phenomena of the seasons. It is possible to argue that they are in themselves phases which are evoked by external changes and that for the purpose at present in view there is nothing to be gained by attempting to consider them as if they had an independent existence : on this view physiological stimuli of the kind in question are merely indirect seasonal stimuli, and an attempt to separate the two aspects will not avail.

It is arguable, nevertheless, that the periodicity of

physiological functions may not be wholly dependent on external seasonal changes. There are examples in the Animal Kingdom (*cf.* Introduction) of functional rhythms which have no such relation, or of rhythms which have such a relation—as those in birds obviously have—but which can retain their periodicity when the influence of the external factors is removed.

Probably it would be nearest the truth to compromise between these two extremes and to say that the rhythmic physiological cycle is related to the totality of the conditions experienced throughout the year rather than to the immediate conditions at given moments. This would obviate the difficulty of the apparent irrelevancy of local environmental conditions in the case, say, of a northern bird wintering on the Equator, where the spring of its native latitudes can have no influence. The existence of a periodicity of this kind is similarly indicated by the fact that some northern birds "winter" in the summer of high latitudes of the Southern Hemisphere while the birds native there are breeding: they experience two summers, with similar external stimuli acting upon them in each, but they breed in only one. In stationary tropical birds, on the other hand, the reproductive cycle is not necessarily an annual one, or different times of year may be the breeding seasons of different species in one and the same area.

There are, then, a number of different possible kinds of answer to the problem with which this chapter deals. The whole answer may lie in external seasonal factors, the whole answer may lie in internal physiological factors, or the whole answer may lie in a combination of the two if, indeed, they can be considered otherwise than as correlated. Again, the answer in respect of autumn migration may be of one kind and that in respect of spring of another. It is even conceivable that the problem is a different one for different species, or for young and old birds of the same species. In any event, enough has been said of the difficulties to show that no one simple answer is likely to be adequate.

Unrest preceding migration

Little evidence is forthcoming from the observational side to help in answering these questions. But whatever may evoke the migration tendency, there is at least evidence that the urge is, when aroused, a very potent force. A great disquiet comes upon the birds until at length they depart:

the flocking and restlessness before departure in autumn are well known in this country in the case of many species. It has also been well described by Hudson with reference to South American migrants: "This same spirit of unrest, or of a "state of nerves," was observable in the majority of the migrants, and manifested itself in an increasing wildness; in signs of suspicion or fear, and extreme readiness to take alarm at slight causes which would not have moved them a short time before. They were like the bird population of a marsh or copse or plain where a hawk has suddenly descended to strike down and carry one of them off. The excitement was not so acute, but it did not pass away in a little while to leave them at peace, as after the raid of a falcon; it continued from day to day, and increased until the moment of going. This spirit of unrest was not visible in all the migrants; it was most marked in the most volatile species, the swiftest of wing and wildest; in others in a less degree, down to those in which it was not noticeable. There were, in fact, with regard to this, as well as to other emotions which birds experience, demonstrative and undemonstrative species. . . . We see then that all this, that what I have called 'The Passion of Migration' is an emotion which accompanies the instinct, the act; that it is fear, and is not the cause but an effect (an incidental effect, one may say) of the impulse impelling birds to migrate."

Even in captive birds—birds, too, which have never known migration in their individual lives—this restlessness has often been observed in high degree. This forms, indeed, the theme of the well-known lines placed at the beginning of this chapter. (The ornithologist must not pedantically refuse the poet licence to speak of vocal powers of a kind which are notoriously lacking in the case of *Ciconia ciconia*!) These cases are not all to be explained, as in the poem, by the stimulus of the sight of wild birds, for this factor has been excluded in many recorded cases. Haecker, too, has found some evidence of a relation between occurrences of this kind and meteorological conditions known to be effective in normal circumstances.

One may well concur with Hudson, however, in saying that the unrest is an effect or symptom of the awakened tendency, and consideration of it does not, indeed, lead much nearer to the answer to the problem: What stimulus is it which at the appropriate times arouses to activity the irresistible urge which forms part of the inheritance of migratory birds?

General conclusions

Although a simple answer is not possible, one may perhaps make a general statement, including and combining all the apparent possible factors, which is likely to contain although not narrowly to define the truth. It is to be imagined that the stimuli which evoke the migration custom exist somewhere in that double cycle of events which is made up on the one hand by the annual seasonal changes of the external world, and, on the other hand, by the annual physiological alternations in the bird itself, these two aspects being closely linked together.

The autumn migration is heralded by the first signs of approaching winter in the physical realm, by the falling temperature, the shortening daylight, and the decreasing food supply. Something in these factors may produce the first symptoms of that unrest which is the prelude to migration. But the advent of this unrest may also be conditioned by the claims of other tendencies or the inhibitory effect of other functions—the necessity for completing the activities of the nesting season, or, in some cases, of delaying until the autumn moult is over. Not until these claims are satisfied, as a rule, will the unrest obtain full sway, although in some cases the restraint may at last be broken and late broods of young be abandoned. Once under the dominion of the unrest only a final stimulus is needed, the occurrence of those meteorological conditions which are favourable for flight : then at length departure takes place. On this theory there is thus a general combination of primary or preparatory stimuli which approximately determines the occurrence of migration at a certain time of year, and which perhaps explains the earlier departure of young birds in many cases, and a particular, secondary, or effective stimulus which finally determines the exact date of departure, and which possibly operates at each successive stage of the journey.

In the case of spring migration the question seems more difficult. Birds which winter in merely temperate latitudes may be stimulated in part by the rising temperature, lengthening daylight, and increasing food supply ; birds which winter in the Tropics would seem to be beyond the direct influence of these factors ; and birds which " winter " in the summer of the opposite hemisphere will as a prelude to their spring migration be subject to the external con-

ditions of autumn. One still inclines, indeed, to lay most stress on the physiological factor in the case of the spring migration and to attribute the main stimulus to the recrudescence of reproductive activity. At the same time it has to be remembered that this recrudescence is part of an annual rhythm which is imposed on the organism by the sum of the external seasonal changes experienced throughout the year and is thus related to the conditions of the summer range : were it not so it would be difficult to see why birds wintering in the Tropics, where the native birds may have a rhythm which is not even annual, or wintering in the opposite hemisphere where the native birds have a rhythm exactly the reverse, should approach reproductive activity at what is spring not where they are but in their still distant summer home. Again, also, one has to note the objection that there exists, in some sort at least, a spring migration of immature birds in species which take more than one year to reach reproductive age. Whatever the general combination of stimuli which approximately determines the time of year for the return migration, there would again seem to be a particular, secondary, or effective stimulus, in the shape of meteorological conditions similar to those which are favourable in autumn, which influences the exact date of departure.

Finally, it is necessary to say that in this chapter the writer again leaves untouched the general question of the nature of inherited customs and of the means by which appropriate stimuli may evoke them to active expression. It is merely assumed that given the inherent tendency and the necessary stimuli the effect is somehow produced.

SUMMARY

Migration is assumed to be an inherited custom which is awakened semi-annually to active expression. Forces which are insufficient as compelling causes may act as releasing stimuli or " occasional causes." The sources of stimulus may be external or internal. The stimuli may be climatic or other factors arising in the cycle of seasonal changes in the physical world : or they may be physiological factors arising in the cycle of alternation between reproductive and non-reproductive phases. The two are not altogether separable, as the physiological changes represent, to some extent, a rhythm imposed by external changes. Difficulties exist in the way of any simple explanation. A combination of various influences is suggested, possibly with a predominance of external factors in autumn and of internal

factors in spring. The unrest preceding migration is probably a first symptom of the effect of the stimulus. There is reason to suppose that there are general, primary, or preparatory stimulating factors which produce this unrest, and a particular, secondary, or effective stimulus, in the shape of meteorological conditions favourable to flight, which leads to actual departure. It may be that the secondary stimulus operates again at the beginning of each stage of the journey.

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CHAPTER XX

FACTORS DETERMINING THE PATH AND GOAL OF MIGRATION FLIGHT

" Yea, the stork in the heaven knoweth her appointed times ; and the turtle and the crane and the swallow observe the time of their coming."

JEREMIAH, viii, 7.

Problems previously discussed leave untouched the actual *modus operandi* of migration—What determines the path of migration flight and what guides the migrants along it ?—Preliminary assumptions : the path not determined by external physical forces—The path and goal are to some extent a part of the racial custom—An hereditary factor must be assumed in the case of unguided flight of young birds —" Inherited memory "—Possible guiding factors discussed— Vision—Other senses—A " magnetic sense "—The idea of a special " sense of direction "—" Homing " of pigeons and other birds— " Homing " only a partial analogy—Further information required —Summary.

GRANTED that a useful purpose is served by migration, granted that some originating cause in the past implanted this form of behaviour in the race, and granted that certain annually recurring stimuli lead to active expression of the custom in the individual, there still remains a problem—or perhaps a series of problems—as to the actual performance of migration.

One may partly express this problem in the question, " How do migrants find their way ? " and in the further question, striking deeper, " What determines the way to be found ? " In more objective terms, and reversing the order of the questions, what determines the path and goal of migration flight, and what guides the migrants along that path and arrests them at that goal ?

Preliminary assumptions

In dealing with these questions it is first necessary to point out that it is assumed that migration has a definite path and a definite goal, and is not in any way haphazard or to an important extent variable from year to year. This assumption would probably be incorrect in some instances,

but all the evidence points to its accuracy in the case of migration of the more highly developed type. The movements of the typical migrants appear to be very regular in their directions and their destinations. It, therefore, seems justifiable to regard the path and goal of typical migration as being largely predetermined, and to ask what the original determining factors may have been and by what means they or other factors still operate to produce the constant phenomena which are known.

One is brought back again to a question already discussed, namely, whether migration can be regarded as the product, created afresh each season, of outward forces of the physical world. This view has been totally rejected in the main as being inconsistent with the known facts, but it might still be argued that external forces, although they do not produce migration, nevertheless determine the details of its course. In other words, it might be true that migration is the expression of an innate custom, but that once the bird rises in the air for its migration flight it becomes the sport of external forces. This theory, however, seems to be quite untenable, because of the absence of any external forces acting with sufficient constancy from year to year to produce the regular phenomena of migration.

Wind, for instance, will not account for the directions of migration flight. These directions are, broadly speaking, the same at particular seasons year after year, and a given journey may be performed on different occasions with a head wind, a tail wind, or with the wind coming obliquely or at right angles from either side. Nor can one find any other meteorological factor which is sufficiently constant in its manifestations to be correlated with the regular sequence of bird movements.

Some have been led to seek an explanation of this kind in the phenomena of terrestrial magnetism. Cathelin, for instance, has propounded a theory of migration which reduces the birds to the status of mere automata acting under the compulsion of "des grands courants aériens electro-magnétiques équinoxiaux." Unfortunately for his argument it is based on a conception of migration which is inconsistent with many of the well-established facts—*cf.* "Le retour au nid reste donc pour nous une des grandes hérésies ornithologiques" (*sic*)—and it presupposes the existence of physical factors as to which the physicists are silent! Nor is its credibility increased by the absence of any suggestion as to a possible physiological nexus linking

the supposed physical causes to the alleged biological effects.

From a survey of these and other suggestions of similar tendency one may readily conclude that there is no known physical cause sufficient to explain the course of migration flight as a thing imposed upon the bird by external forces.

It might be argued that, although the course of migration is regular and predetermined, it is not fixed in a topographical sense but only in its main directions with reference to geographical factors of a very general kind. In this way the path of migration would not be regarded as being from this country to that or across a particular sea, but as being from north to south, or from cold to warmth, or from dark to light. The direction of flight could thus be explained on tropistic lines, a point to be discussed more fully in the succeeding chapter.

This view, however, seems also to be untenable in the face of the known facts. Migration does not always follow straight lines, but often finds its goal by an indirect path. These paths, moreover, are not the same for all birds, and may cross each other at right angles. Everything, indeed, points to the course of migration being determined in much more detail and with much more complexity than can be explained by factors of so general a kind as those indicated. The path of flight appears very often to consist of a definite route which is determined in relation to the main topographical features of land and sea. The routes may follow coast-lines, for instance, or may cross intervening seas at particular points. This is not, of course, to say that the routes are necessarily fixed with great accuracy with reference to minor topographical features, or that all migratory birds are restricted to a small number of common paths.

The hereditary factor

Taking all in all, there seems to be no escape from the conclusion that following a more or less definite path to a more or less definite goal is a part of the inherited custom, and that the path and goal were determined either when the custom originated in the race or in the course of its subsequent evolution: this is not to say that there may not be a considerable margin of error within which deviation of path or variation of goal may safely be made. It does not even seem possible to regard this part of the custom as traditional rather than hereditary, in view of the known

independent migrations of young birds in many cases: these lack both direct experience and the guidance of experienced individuals, as well as all those aids which human beings would have in intelligently fulfilling a conscious purpose. It has been held that there must be racial memory, "inherited but unconscious experience," and to this conclusion it does not seem easy to dissent, despite the difficulties involved, in the absence of any good alternative. Individual memory, of course, may well be superadded in the case of older birds, and there are instances in which tradition—the imitation of old by young—may well play a part. In this regard Lucanus quotes instances in which parties of young birds reared in captivity but allowed their freedom have shown unrest in autumn, and have taken frequent short flights in the neighbourhood, but have not migrated. This is ascribed to the absence of parents or to the fact that these, when present, were pinioned. The records refer, however, to birds, such as Geese, which are known to travel in family parties, and in any event one does not necessarily attach importance to the behaviour of birds not wholly subject to natural conditions.

One may be reluctant to accept so difficult an idea as that of "inherited memory": some have, indeed, dogmatically asserted its impossibility. Yet even so, it would seem that the operation of an hereditary factor must still be admitted in more general terms. The most mechanical explanation of the act of migration which would be at all consistent with the known facts, would necessarily include some recognition of this aspect of the matter. Generation after generation of young Cuckoos, to take an example where tradition is very clearly excluded, perform an autumn migration which, at least in its main features, remains true to type. Either, then, the bird is a mere passive thing affected by some external forces of a complex yet constant nature of which the physicists have at present no knowledge, or the performance of the act is in some way determined to an important extent by the bird's inheritance. The use of the words "knowledge" and "memory" may be avoided, as having too difficult implications, but it remains necessary to assume that factors which to some extent determine the path and goal of migration flight may, and sometimes do, form part of the bird's inborn nature.

It seems necessary, at least in the present state of knowledge, to make this assumption, although it must be admitted that difficulties exist. One of these which arises from

the facts of migration itself may be briefly mentioned, namely, that of differences in behaviour between individual birds of the same species native to the same area. As stated in a previous chapter, the marking method has clearly shown that, for instance, among Lapwings bred in Aberdeenshire and the neighbouring counties some winter there, some in Ireland, and some in Portugal. Theoretically, the question seems to present itself in two alternative forms. If the racial custom is similarly inherited by all the birds, what is it that stimulates it to greater activity, or to different activity, as between one individual and another ? Or if different customs, or different degrees of the same custom, are inherited, how can this be accounted for —are there various *gentes* not morphologically distinguishable but differing in constitution and temperament in ways not at present definable as, for instance, a resident *gens*, an Ireland-seeking *gens*, and a Portugal-seeking *gens* ? If it could be assumed, which it cannot with any certainty, that Ireland lies on the route taken by the birds making for Portugal, the question would be greatly simplified : difference in kind would be eliminated and only differences in the degree of performance would be left. It may also be remarked that evidence is lacking as to whether, in cases like this, any given individual behaves in the same way in successive years : in any event, however, it may be supposed that experience plays some part after the first occasion and that the behaviour of some individuals of a gregarious species may at times be largely imitative. In the absence of greater knowledge, speculation on these lines is not at present likely to lead any further.

Assuming, therefore, that a knowledge of the path and goal of migration is in some way inborn, and ignoring for the present the deeper implications of this view, one is left with the more tangible problem as to how the migrants are guided along this path. If the route is " known," how is it found and followed ? What senses are involved to provide the necessary link between the subjective knowledge or " awareness " of the route and the objective facts themselves ? Is the course steered by landmarks recognised by vision or by other factors perceived in some more subtle way ?

Vision

The arguments against the vision theory are chiefly that much migration takes place by night and that stretches of

open sea are commonly crossed. The former is not necessarily a serious objection: the darkness of the night is never absolute and birds have a notoriously acute vision, while such features as coast-lines and rivers are just those which are most likely to be visible in the faintest light.

The sea crossing is a more important point and one that cannot be overcome by suggesting that birds fly at such a height that they are able to keep land in sight all the way. It may be pointed out in this regard that from 500 feet above sea-level a bird would be able to see low-lying land 29 miles away; from 1000 feet, 41 miles away; from 3000 feet, 72 miles; from 5000 feet, 93 miles; from 10,000 feet, 131 miles; and from 25,000 feet, 208 miles; mountains would be visible at greater distances. These figures allow for the refraction of light rays of the ordinary visual values. It has, however, been suggested that birds may be able to utilise light rays which are outside the limits of human visual perception and which are so strongly refracted by the atmosphere that the curvature of the earth's surface is practically eliminated: even had this theory a sound physical basis, it would seem to be negatived by physiological tests which have been made by Watson. Account must also be taken of the limits imposed by the degree of acuity, that is of the power of appreciating small or distant objects: by human beings points separated by less than thirty seconds of arc cannot be separately distinguished, but corresponding data for birds are lacking.

From figures similar to those just given, Meinertzhagen has stated the conclusion that in most parts of Europe or Asia an elevation of 5000 feet would suffice for the picking up of landmarks, although in the case of some of the migrants which cross the Pacific Ocean a quite impossible altitude of over seventy miles would become necessary to satisfy the theory. As the same writer justly observes, however, there is no occasion to suppose that landmarks must be kept in sight, insomuch as we know that many migrants habitually fly at very low altitudes over wide expanses of sea. Under conditions of visibility such as commonly obtain on the North Sea the low-flying migrants have an horizon of a very few miles even by day. It is therefore necessary to believe that migrants can cross the sea without landmarks.

The arguments in favour of the vision theory seem to be important. On the one hand it is known that migrants readily lose their way in fog and are commonly delayed by

foggy conditions. It is also believed that birds prefer to fly below the cloud level, especially where there is a continuous stratum of cloud. Migrating birds, also, may often be observed to follow features of the landscape with accuracy, and an instance in which migrating flocks were seen by the present writer to adjust their flight to a bend in the coast-line has already been quoted (Chapter III).

It seems, therefore, that migrants are guided at times by visible landmarks; that even at night coast-lines and rivers at least may often be visible to them; and that the concealment of landmarks by fog is apparently disturbing. The writer is accordingly inclined to regard vision as of high importance in this respect, while fully admitting that birds cross the sea without landmarks. It may be that in sea crossings vision, taking account of the sun or stars, of the set of the waves, or of the direction of currents, is useful in helping to steer a course of which the initial direction is determined by landmarks on the coast of departure. In the case of most sea crossings, also, there must be a wide margin of error available, because the farther coast need not necessarily be struck exactly at any particular point.

Lucanus has indeed suggested that the orientation of migrants is of two distinct kinds, "gross" and "fine": Schenk prefers to term them "primary" and "secondary." The one takes place by means of a faculty for maintaining a constant direction of flight when once begun, and the other consists in the following of visible landmarks. The idea is a tempting one, as offering some solution of the difficulty just discussed. In the present state of knowledge, however, one must be careful lest the introduction of a purely speculative complexity should obscure the real problem.

Other senses

Whether or not any other of the ordinary senses may play a part in path finding is very doubtful. Hearing might conceivably play an accessory part in, say, following a coast-line on a very dark night, but it could not well be important. Similarly, windborne smells might just possibly give occasional indications of the direction of unseen land or sea. The temperature or humidity of air currents might also be a partial guide at times, and there is Cyon's theory that the direction, strength, and temperature of the wind as it plays on the olfactory mucous membrane may assist flying birds to find their way: against this theory, however,

there is the evidence of Watson and Lashley, who found in their experiments, presently to be described, that Terns retained their powers of " homing " even if the nasal cavities were filled with soft wax and varnished over. It seems unlikely, indeed, that any ordinary sense except that of vision could play a sufficient part to contribute greatly to the solution of the question of route finding.

The writer has used the expression " ordinary sense " so that he should not be thought to prejudge the various theories which invoke some additional sense as yet unknown to physiology. These theories seem to be of two kinds, sometimes confused in the looseness of terminology which is too often to be found in discussions of these intangible ideas. On the one hand there is the definite theory of a " magnetic sense," *i.e.* of a power of perceiving the phenomena of terrestrial magnetism and of using them for purposes of orientation, and on the other hand there is the vague idea of a " sense of direction," *per se*, which does little more than give a new name to an old mystery. These two may be taken in turn.

" Magnetic sense "

The possible existence of a " magnetic sense " in animals has for long been a subject of speculation, and Kelvin is numbered among those to whom the idea has proved attractive. No direct evidence in its favour has ever been obtained, but on the other hand there is no actual proof that some form of physiological sensibility to the phenomena of terrestrial magnetism may not exist and be a factor in the power of geographical orientation which is displayed by many animals and by primitive man. The idea has often been invoked in the case of the especially remarkable powers of orientation which are possessed by migratory birds and by homing pigeons, and it is with reference to the latter that the theory has been worked out by Rochon-Duvigneaud and Maurain, a biologist and physicist in collaboration. This is here taken as an example of theories of this kind, but similar views have been expressed by Viguier and others.

Maurain's suggestion may be stated as follows. The magnetic declination (angle of magnetic needle's lateral deviation from the geographical meridian) and the magnetic dip or inclination (angle of needle's deviation from the horizontal plane) both vary from place to place over the surface of the globe. The periodical variations at any given place

and the irregular disturbances which also occur are small in proportion to the otherwise constant geographical differences. Roughly speaking, therefore, every locality has its characteristic declination and dip. If lines be drawn through the places having the same declination and other lines through those having the same dip, these lines are, in Europe, roughly at right angles to each other. The lines thus serve as co-ordinates which fix the position of any given locality like lines of longitude and latitude. Moreover, the declination and dip increase or decrease progressively as distance from a given locality is increased, except along those lines where one or other factor remains constant.

It has then to be supposed that the pigeons are sensitive to changes in declination and dip, and indeed simultaneously sensitive to each factor independently of the other, and that when removed to a new locality the birds have a natural tendency, so to speak, to seek their own magnetic level. If a pigeon be removed to another place having the same declination but a greater (or less) dip it would fly along the line of equal declination in the direction of decreasing (or increasing) dip. Similarly, if removed to a place having the same dip it would follow the direction in which the declination changes towards the amount found at the home locality. Again, in the more general case of a bird removed to a place where both declination and dip are different, it would be affected by both factors and its homeward path would be the resultant of the two tendencies. (It is remarked by the authors that there is no question of remembering the magnetic changes experienced on the outward journey, as they believe that a bird removed by a circuitous route finds a direct path home.)

Ornithologists will be grateful to the physicist for the statement of a possible case, but they will regret that Maurain has confined his argument to the relatively short journeys performed by homing pigeons and to the possible magnetic factors as they exist in Europe, for it is not in every part of the world that the lines of equal declination and of equal dip run at right angles to each other, and that there is only one point at which a given pair of values for these factors is to be found. They would have liked to see a case similarly stated in respect of the migration of, say, Swallows from South Africa to England over an area in which more complicated changes in terrestrial magnetism have to be reckoned with: an ever-increasing volume of records of marked birds shows that Swallows and others

commonly perform very accurate feats of " homing " from great distances.

Returning to homing pigeons, however, the argument may be examined more closely. The physical phenomena exist, and a remarkable power of orientation is undoubtedly involved in homing: can a connection be traced between them? The most serious objection seems to be the entire absence of any evidence of sensibility to magnetism on the part of birds or other animals, and without this physiological link speculation must needs be barren. Kelvin got negative results from his experiment of subjecting the human head to the influence of a powerful magnetic field; Du Bois observed no effect on protozoa; and the writers of the paper under discussion have similarly failed with pigeons. Within a limited field, it must be remembered, the strong electro-magnets used in such experiments are very many times more powerful than terrestrial magnetism. Yet for Maurain's hypothesis it must be supposed not only that birds are sensitive to minute changes in terrestrial magnetism, but also to changes in two of its factors separately.

One must conclude that although the idea of a " magnetic sense " is capable of reduction to concrete terms, when this is done it loses much of its first attraction in face of the difficulties which become apparent in the course of detailed examination. Even should a magnetic sense exist it would not in itself suffice in the case of migration. The capacity for perceiving magnetic directions would alone be no more serviceable to a migrant than would be a compass to a human being not also possessed of a map or at least of a mental picture of the country to be traversed. The magnetic indications must not only be perceived but must also be brought into due relation with the essential geographical facts.

" Sense of direction "

There remains the rather intangible idea of a special " sense of direction." The expression is ambiguous, especially in the inclusion of the word " sense," and has been given different meanings. By some it has been used as synonymous with " magnetic sense," which need not be further discussed. By its original users, in application to migration theory, it was intended merely to indicate the undoubted existence of a highly developed power of orientation, and by others it has been used to include the idea of racial memory or inherited experience, to which reference has already been

made: used thus it serves merely as a label for a factor which is not fully understood. Unfortunately, the expression has also been used by some as being in some mysterious way explanatory, and as denoting the existence of an additional "sense" in the physiological meaning of the word. Consideration in detail reveals ground for doubt as to whether any useful meaning can be attached to the expression when employed in this way, but the vague idea behind it has enough popular currency to make some discussion of it necessary.

When one speaks of a person as having "a good sense of direction"—or "a strong bump of locality"—one does not imply the existence of any special channel of perception but merely acuteness in perceiving certain things by the ordinary senses and ability in co-ordinating the impressions in a useful way. Good observational powers, a good topographical memory, and a power of visualising country are involved: there may also be memory of the turns and movements made. Thus by conscious or subconscious observation and memory one is provided with the data for orientating oneself with reference to a known point from which one has travelled. Great differences are noticeable in this respect between one person and another. One man will be able to leave his hotel in a strange city and after some hours of walking in, say, a semicircle, will be able to find his way back by a short cut: another will in the same circumstances have no idea how he stands in relation to his starting-point, because his mind has not registered the distances and directions of his progress or, if it has, he has no power of constructing a mental map from the data. In the open other factors come into play, for various landmarks may be visible throughout and so help to give his bearings to a man with "a good eye for country."

With such variations between one person and another in civilised races, it is not surprising to find a great difference between the powers of civilised man in general and primitive man. In the latter the observation, memory registration, and visualisation are probably less conscious than in civilised man, and from constant use and development the faculty is instinctively exercised. So also, *a fortiori*, in animals.

The "sense of direction" is therefore, in this view, not a special sense in itself but is a faculty for co-ordinating impressions received through the ordinary sense channels and relying, in its high development in animals, on the great acuity of these.

To imagine a special sense by which direction is perceived implies two things. On the one hand there must be some special physiological channel of perception, and of that there is no evidence. On the other hand direction must be reduced in some way to objective terms as a thing capable of direct perception. Direction, however, is not an entity like light or sound or gravity, but is merely the relationship between different points. Each of these points has its physical characteristics which make their impressions on the senses, but the relationship between them cannot be thought of in this way. One can accordingly attach no meaning to the expression " sense of direction " (apart from the possible sense of magnetic direction already discussed), if it be used to indicate more than acuteness of ordinary sense perceptions coupled with a power of co-ordinating the resultant impressions as an aid to orientation.

Granted that birds have remarkable powers of orientation, one can understand their finding a known route or even their finding a new route back to a known point. But it has to be assumed that the route or the general direction of the destination is indeed known : this implies the assumption already made, namely that in the case of the first autumn migration performed by young birds alone there must be inherited " knowledge," as individual memory or traditional knowledge seems often to be excluded. In all other cases there is, of course, some individual memory and the performance is one of repetition. Even if the return journey be by a different route the first spring migration is at least between two points of which the relationship is known.

One further special theory may be mentioned under this heading. Dewitz (quoted by Lucanus) has propounded the view that birds have some special power of orientating themselves in relation to the quarters of the heavens and that migration usually takes place towards one or other of the four cardinal points. This theory, as it stands, certainly cannot be reconciled with the facts, whatever may happen to be the appearance in the particular locality where the special observations were made. At the same time it does not seem extravagant to suppose that such things as the position of the sun in the heavens may play a part in orientation. This is, however, no solution of the problem, the previously cited analogy of the uselessness of a compass without a map being here equally relevant.

"Homing"

The facts about the homing of pigeons which are of chief interest to ornithologists have been usefully summarised by Riviere, and some account of them, chiefly from that source, may here be given as an aid to consideration of the question under discussion. The homing pigeon is, of course, one of the breeds of the domesticated variety of the Rock-Dove (*Columba livia*), a species which is as a rule non-migratory in the wild state. First-class homing powers are shown only by birds which are the result of careful selective breeding, and the standard of performance has been steadily improved as this has proceeded. Even so the training of the individual bird is very important, and is accompanied by heavy loss : only some five per cent survive to achieve the longer flights, very many birds going astray or otherwise perishing.

Racing pigeons are always trained in a given direction from the loft and thus always have to "home" in approximately the same geographical direction. Very short distances are first tried, and these are increased by easy stages until the young bird can take part in races of 150–200 miles ; as yearlings they manage greater distances. As the distances are increased the individual "jumps" are also increased, so that a point is reached when a bird may have to fly as much as 100–150 miles over new country before picking up the route of previous training.

The adults fly courses of 500 miles or more, and the record flight for a single day seems to be 634 miles, which was accomplished in 18¼ hours. Mention of the velocities recorded has already been made in an earlier chapter.

Greater distances are covered in flights lasting more than one day. A pigeon released at Rome reached its loft at Derby, 1001 miles, on the thirty-third day : it was one of only two out of 106 which accomplished the journey at all. One remarkable bird did the distance from Barcelona to Brussels, some 700 miles, twice during a period of three weeks and in all eight times in five seasons. In America, where long overland courses are available, distances of 1000 miles or over are more frequently and more quickly flown. Pigeons have been successfully raced from ships as much as 125 miles out at sea.

One notices that it is a feature of the records that what seem to be disproportionately long times are commonly required for the longer distances. Thus a distance which

is only double that of an ordinary single-day race may often take the best birds a week or even a month to cover. This seems to suggest that wide stretches of country may be covered in the search for known landmarks, although delay may also be due to the birds being held captive at other lofts where they have sought refuge. Quicker times over long courses may be the result of better training over intermediate distances: the world's long-distance record for homing pigeons is said to be 1010 English miles covered (in America) in $35\frac{1}{2}$ hours, which must have included stoppage at least during the night, and, therefore, indicates a fairly direct line of return.

In all ordinary records of homing performances it may be assumed that the birds have been previously flown over at least a great part of the course, and that they have been trained for flight in the particular direction required. Furthermore, the less trained birds may be guided to some extent by the more experienced ones taking part in the race, for the pigeons apparently fly in company as much as possible: it is known that lofts rather out of the main course of a big race stand a poor chance of recording good times, because of the "drag" of the other birds. What can be done in a direction different from that of training is known only from a few cases. Thus, for instance, a bird bred in Lancashire and trained over a course of 50 miles to the south was bought by a Thurso dealer: it escaped and found its way back from the north of Scotland to its original loft, some 250 miles, in one or two days. In a similar case the return was from Dublin to Belgium. Riviere considers that instances of this kind may be purely fortuitous, and negligible when compared with the great numbers of birds which lose their way even in ordinary flights. The experiments of Thauzies on this point, however, suggest that the matter cannot be thus dismissed. At Geneva, during the session of an international psychological congress there, he released birds belonging respectively to Versailles, Guéret (Creuse), and Gannat (Allier), the last two localities being in the centre of France and approximately west of Geneva. None of the birds had been flown from Geneva previously: the Versailles' birds had been trained from the Brest direction, the Guéret birds from the Amsterdam direction, and some of the Gannat birds had previously flown from Mâcon. There were sixty-six birds in all, and the three sets were released at short intervals on the same morning. Two reached Versailles and two Guéret on the same day, most of the

others were home the next day and all but one within the week.

It is quite certain that vision and topographical memory play a large part. Unlike many migrants, homing pigeons fly only by day. On release the birds usually circle up to a height and can often be seen looking in all directions before choosing the line of flight. In fog the birds are quite unable to find their way, even from distances of two or three miles, and this seems to be a particularly important point: thunderstorms are also unfavourable. In general it seems to be agreed that good conditions of visibility mean good returns.

An interesting case in this regard is that of a bird bred in Antwerp and trained at first over a course through north-eastern France: it was then purchased and brought to Manchester, where it was given time to become accustomed to the new loft, and was then trained over a southerly course with local birds. For two seasons it raced from the Straits of Dover to Manchester in good times. It was then taken a stage farther and raced from Arras. Here, apparently, it picked up the "road" it had learned in its earlier days, and it found its way back to its original loft at Antwerp. Further evidence may be deduced from the fact that when a pigeon gets lost and returns by a roundabout route it may persist in following that route on subsequent occasions, and so becomes useless for racing purposes.

Pigeons can be trained to "home" to a movable loft from short distances, a point of much practical importance in the military use of the birds. Usually the loft is not moved except with the birds in it, but when a loft has been experimentally moved a few miles in their absence they have found their way back. Vision is obviously the important factor in these cases.

There remains the question as to how orientation is effected when the bird flies for the first time over an increased course, when, say, the first hundred miles are new to it and may include an expanse of sea. It seems necessary to assume that the bird's training enables it to take up the correct general direction and to follow it until known landmarks come into view. This does not imply that the direction is recognised owing to any "magnetic sense," such as has already been discussed in some detail earlier in this chapter. There are other ways in which direction can be recognised, such as by the sun, and the direction in which the pigeon flies is always the same one. (It will be

remembered that the magnetic theory rather assumed that the pigeon could find its way from any quarter.) The difficulties in the way of the idea of a mysterious "sense of direction" also do not apply, for here the direction to be found has an objective existence, and is not a question of the relationship between any unknown point and a known one.

A theory of homing which deserves mention is that of "contrepied," which is based on the assumption that the birds are able to register the distances and directions travelled on the outward journey, even although they are taken in covered baskets and in closed vehicles. In support of this it has been claimed that pigeons belonging to the French military service have been taken out in this manner by a devious route and have flown home by the same path: but Watson and Lashley have been unable to find in the literature of the subject any satisfactory account of such an experiment. The same writers quote experiments by Exner in which pigeons have been anæsthetised, or rotated, or subjected to electrical stimulation of the labyrinth region —the supposed seat of the function—during the outward journey: the birds homed as satisfactorily as the normal control birds taken out at the same time but separately released.

There would still seem to be a promising field for experiment in regard to the homing of pigeons. The performances of relatively untrained birds, and of birds flown in directions other than that of training, require further investigation. The behaviour of birds trained simultaneously in more than one direction, if that be possible, or of birds trained over an increasing course which is not a straight line, would also be interesting. In experiments the birds should, of course, be flown singly to avoid the influence of other birds such as occurs in big races: it is necessary to eliminate the possibly large traditional factor which is introduced by the flying of the less and the more practised birds at the same time.

In addition to the records of "homing pigeons," and to the many tales of domesticated mammals returning after removal to a distance, there are on record some interesting experiments with wild birds. Among these may be mentioned those of Watson and Lashley, who took as their special subjects the Noddy Terns (*Anous stolidus*) and Sooty Terns (*Sterna fuscata*) nesting on the Tortugas Islands in the Gulf of Mexico. Breeding birds taken from their nests

and transported by ship in closed cages were shown to be capable of finding their way back from Galveston (to the east) or from Cape Hatteras (to the north), distances of over 850 miles, or from intermediate points at sea entirely out of sight of landmarks of any kind. When taken northwards, too, the birds were removed beyond the limits of the species' natural range, and the absence of any previous experience in that direction was thus all the more certain.

It is necessary, however, to remember that the problem is not wholly the same as that of direction-finding in migration. In migration there is this difference to be noted between the autumn and the spring flight: the autumn journey is performed for the first time over a path and to a goal new to the individual, while the spring journey is made to a known goal, and, unless a different route be adopted, over a previously traversed path. "Homing" flight, following removal by artificial means, is not strictly analogous, even apart from the obvious absence of any racial memory element, to either the autumn or spring flight in migration: "homing" takes place to a known goal, recognisable when reached, but over a route which may not previously have been traversed in flight.

It must, therefore, be admitted that the available evidence as to homing, both in the case of domestic pigeons and of experiments with wild birds, is not very helpful. It may even seem that it introduces a difficulty, in that the remarkable performances recorded are not explicable by assuming an hereditary factor; for in their special features, as distinct from their general nature, they are new or partly new in the case of the individual bird under observation. The point has, indeed, been used as an argument with regard to migration, but this line of reasoning does not seem to be wholly valid. For one thing, it is an argument from analogy, notoriously a dangerous step in logic, and it has been seen that the analogy is at best a partial one. For another thing, the recorded performances in question refer to much smaller distances than have in many instances to be considered in dealing with migration, and it is thus possible that some simpler explanation may in these cases be found to cover the facts.

Further information required

More experiments should certainly be made, and these should, if possible, be extended to include true acts of migration. For example, one may mention an experiment

with Storks (*Ciconia ciconia*), which has been suggested by Schenk. As has already been mentioned (Chapter X), there is evidence to show that birds of this species in one part of the European breeding range migrate south-eastwards in autumn, while those in another part travel south-westwards. The suggestion is that eggs laid in one region should be transferred to nests in the other, and that the migrations of the young birds be then studied by the marking method. The result might be of much interest, but there are possible sources of fallacy. In the first place it would be necessary to have much more evidence than yet exists as to the normal facts. Reference to the account of this evidence already given will show that it is too soon to be certain that the direction of departure in this case differs in a constant manner as between two definite native areas ; and in any event the limits of these supposed areas are still unknown. An experiment is obviously valueless in the absence of normal " controls." In the second place, there is the possibility, especially in the case of a gregarious species, that a few birds abnormally placed would become merely imitative in their behaviour : it would be of great interest if the youngsters followed the custom of their real parents, but if they conformed to that of their foster-parents and foster-brothers no certain deduction could be made.

The question involved, it may be added, is closely similar to that already discussed in this chapter with regard to the Lapwing.

Apart from deliberate experiments, something might be learnt from observation of the behaviour of birds of species which have been introduced by human agency into entirely new regions where none of their kind are indigenous. The evidence at present existing on this point appears to be very meagre. In any event there is the difficulty of the absence of any normal standard of comparison : a migratory species in a new region, as, for example, a European bird introduced into North America, might conceivably achieve migration of a kind, probably with a lack of definiteness as to direction and as to the site of winter quarters, in spite of the fact that the performance of its migration in its proper area was largely determined by the hereditary factors which are presumed to be the cause of the constancy of the annual picture.

Furthermore, there is still much that is relevant to the problem which can be learnt from the study of migration itself. It is known that in a general way the directions

and the destinations of the migrations of various species are constant, but one has as yet little information of a more detailed kind, and is, for instance, ignorant of the range of variation which exists between individuals, or between performances of the same individual in different years. One is unaware of the exact nature of migration routes or of the degree of accuracy with which they may be followed. Without more information on points such as these it is not likely that any great advance will be made towards the solution of the problem which has been dealt with in this chapter.

SUMMARY

Granted that the racial custom of migration serves a useful purpose, was originated by some compelling cause in the past, and is evoked to active expression by some recurring stimuli, the *modus operandi* of the actual performance remains as an additional problem. No external physical forces exist which seem adequate as factors determining the path and goal of migration flight in its more highly developed forms. The paths of migration are known to be both relatively constant and very complex, and a capacity for following more or less definite paths must be regarded as part of the inherited custom. It thus seems difficult to avoid the conclusion that there is some inherited memory of the path and goal, as the knowledge cannot be traditional where young birds migrate for the first time unguided. Assuming that the path is indicated in some way of this kind, there remains the question as to the means by which it is followed. There seems to be reason to consider vision as important, although it may seem inadequate in the case of the over-sea paths: the adverse effect of fog is to be specially noted. Other senses seem unlikely to be important. There is no evidence of a "magnetic sense" and the idea of a special "sense of direction" appears to be devoid of exact meaning. The "homing" of pigeons and other birds removed by artificial means is not strictly analogous to migration, but raises some special points of difficulty.

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CHAPTER XXI

THE WIDER BIOLOGICAL IMPLICATIONS OF MIGRATION PROBLEMS

"While the frequent limitations of instinctive behaviour seem to us to point to a differentia between it and intelligent behaviour we find further evidence in considering its achievements in preparing for the unforeseen and remote—for offspring which will never be seen, for the evasion of a winter which will never be experienced. There is an adjustment of means to ends which certainly does not rest on a basis of individual experience."

J. ARTHUR THOMSON (1920).

Review of the problems of bird-migration—Statement of a partial working hypothesis—Wider biological implications—The nature of inborn predispositions—Reflex actions, tropistic reactions, instinctive behaviour, and intelligent behaviour—Migration problems in the light of the wider issues—Conclusion.

IT has been shown that the known facts of bird-migration raise a number of problems of great theoretical interest, and these have been separately stated and discussed in the preceding chapters. Of these problems, and of the partial answers which may be suggested, some final summary may now be given, and some of their wider biological implications may, in conclusion, be referred to briefly.

Review of the problems of bird-migration

The thesis has been that migration cannot be regarded as the result of intelligent action or as a reasoned course of conduct, and that it cannot be explained as the direct effect of recurring physical changes acting as external compelling forces on almost passive subjects. Migration can be considered, consistently with the known facts, only as the expression of a racial custom and as an example of behaviour largely determined by inheritance.

Migration being an hereditary custom and an expensive one, it must bring some advantage to its possessors or it would not survive: therein the first problem. The racial custom must have been originated in the past history of migratory species by some compelling cause, the nature of which forms the second problem. On each occasion, too,

the custom must be evoked to active expression in the individual by recurring stimuli, and these form the subject of the third problem. Given all these factors, the fourth problem lies in the means by which the actual performance of migration is effected.

Statement of a partial working hypothesis

Migration, then, is to be looked upon as an inborn custom, and as one which is of advantage to its possessors in enabling them to inhabit two different areas at the respective times of year most favourable in each. The advantage of winter absence from high latitudes lies in the avoidance of cold and stormy weather, of the short hours of daylight, and of the scarcity of food. The advantage of return to these latitudes for the summer consists in the availability of suitable breeding-places, in the long hours of daylight, and in abundance of food at the critical period of the year. The existence of these advantages does not in itself, however, explain causation.

The racial custom is to be regarded as having been originated in the far past by some great compelling cause or by some development in the history of birds and of their distribution over the surface of the globe. It may be that some great climatic change or series of changes, such as a glacial epoch, acted as a compelling force and superimposed the custom of migration upon the pre-existing behaviour of birds. It may be that the custom gradually evolved during the natural spread of various species from an original area of resident habitation. Or, again, it is even conceivable that the custom sprang suddenly into being, in one case and then another, as the result of some abrupt effort of range expansion. Whatever the cause, whether coming from without or arising from within, and whether gradual or sudden in its operation, the resulting custom is probably to be regarded as being in some part the repetition by the individual, year after year, of some process or event in the past history of the race.

Given the racial custom, originated by some causative factor in the past, it is necessary to assume the existence also of recurring stimuli which awaken it semi-annually to active expression in the individual. These stimuli may be climatic or other external factors arising in the cycle of seasonal changes in the physical world, or they may be physiological factors arising in the cycle of alternation

between reproductive and non-reproductive phases which makes up the bird's life. Probably the stimuli are a combination of both factors, if, indeed, these could in any case be wholly separate, with perhaps a predominance of the extrinsic element in autumn and of the intrinsic in spring. These primary or preparatory stimuli, whatever their precise nature, produce that unrest which is the first symptom of approaching migration, and a secondary or effective stimulus in the form of favourable meteorological conditions is all that is needed to set migration in actual motion.

The existence of still other factors must be assumed to complete the explanation, namely, those which control the actual performance of migration and which determine for the individual the path and goal of its migration flight. Here one seems practically compelled to admit the possibility of some element of inherited memory of route and destination as part of the racial custom. Assuming this, it seems probable that vision is the chief sense which enables the bird to follow its determined path.

Here, then, is presented in outline not any solution of the problems of bird-migration, but a working hypothesis which attempts to make as near an approach to an explanation of the facts, in general terms, as is possible in the present state of knowledge of the subject. The writer's endeavour has, indeed, been to state the problems as clearly as possible rather than to attempt their solution by an elaboration of theoretical argument. Even the partial answers which have been suggested are open to many objections and raise many difficulties, of which some indication has been given in the fuller discussions in the preceding chapters. This section merely summarises the general lines of explanation which seem to emerge, and indicates the writer's view of the position of migration theory to-day.

Wider biological implications

Even were the possible explanations more complete and more satisfying in themselves, there would remain wider implications and underlying assumptions as subjects for further and more profound speculation. These open up questions of wide biological import in no way peculiar to the special subject of this book, and no more will be done here than to indicate their general nature.

The hypothesis which has been outlined assumes that

migration is an inherited custom. It assumes that this custom had an originating cause, that it is evoked to periodical activity by recurring stimuli, and that in its performance inherited memory of geographical features probably comes into play. The nature of the originating cause of the racial custom, of its evoking stimuli, and of its performance are problems for the student of bird-migration ; but the very statement of these problems raises wider questions in general biology.

What is the nature of an inborn custom, and how is such a mode of behaviour inherited ? How is an inherited custom originated by a given causative force ? How do given stimuli evoke an innate custom to active expression ? By what means is the customary action performed, and how can memory be inherited ?

Reflex actions

When one inquires into the nature of an inherited custom one immediately raises the question of the level of behaviour at which it should be placed. At the bottom of the scale there are those simple reflex actions which are explicable in purely physiological terms, *i.e.* by pre-established linkages of particular sensory neurons, adjustor neurons, motor neurons, and muscle-cells : in general, the constitution of the organism is such that a particular stimulus evokes a particular response, and a definite nexus between cause and effect is discoverable. So complex a form of activity as migration obviously cannot be considered as being on this low level, even allowing for all the possibilities of the combination or sequence of different reflexes into unified actions.

Tropistic reactions or forced movements

Of a more elaborate kind are these obligatory movements, called " tropisms," which more or less automatically secure physiological equilibrium in relation to certain external stimuli. According to Loeb the behaviour of animals is made up of " forced movements " which they are compelled to make by external agents to which they are especially sensitive and to which they have characteristic reactions, and which are positive or negative according to whether the external agent is attractive or repellent in its effect. Thus, some organisms are positively heliotropic (or phototropic), tending to move towards the light ;

others are negatively heliotropic. Galvanotropism is shown by animals which orientate themselves in a particular way relatively to the direction of an electric current. There are also reactions to the stimulus of temperature changes (thermotropism), chemical agents (chemotropism), the contact of physical objects (stereotropism), gravity (geotropism), and the direction of the movement of retinal images (rheotropism).

The explanation Loeb gives of such tropistic reactions is purely a physico-chemical one. The external agents cause certain chemical or physical changes in the tissues of the animal and these find effect in particular actions. It is not a question of pleasurable or painful sensations but of such effects as changes in the tension of particular muscles. The symmetry of the animal body is important, and where there is the common bilateral symmetry the equality or inequality of the stimuli on the respective sides largely determines the direction of movement, the tendency being to produce the adjustments of position necessary to secure equal stimulation of both sides. A positively heliotropic animal, for instance, tends to move not towards the brighter of two equidistant lights but towards a point between the two and proportionately nearer the stronger (resulting from a turning of the body so as to expose a greater lateral surface to the weaker light).

Tropistic reactions are obviously not the mere result of compelling external agents such as might act similarly on inanimate objects, but involve the action of an internal organisation sensitive to the particular form of stimulation. In many cases the internal organs concerned in automatically securing tropistic adjustments are very intricate and delicate and must have taken long to evolve—the statolithic arrangements, for instance, which are of great importance in many animals in securing equilibration. The organism is not necessarily sensitive at all times to the same degree or in the same way, and here the hormone theory comes in. The sexual reactions, for instance, are evoked by the appropriate stimulus only when the animal's body is rendered receptive at particular times.

Where animals possess the faculty of "associative memory," a reaction may be obtained by some stimulus apparently irrelevant to the physiology of the body but associated in memory with the natural stimulus. It was shown by Pavlov, for instance, that the ringing of a bell to which a dog was accustomed at feeding time provoked

a flow of saliva, just as if food had actually been shown to it as before. The reaction was even quantitative, the amount of secretion increasing with the accuracy with which the accustomed sound was reproduced. In this way the theory of tropistic reactions is extended to explain conduct at what might be considered intelligent levels, and its authors even push it to cover conduct at the level of human consciousness, although this extreme does not concern the present question.

Of the observations described by Loeb one of the most interesting for the present purpose is that made on bees in an observation hive built of glass but usually kept under a dark cover. At swarming time the bees began to issue from the opening at the foot of one side where the only light came in. But when the cover was removed they all rushed towards the brigher light at the top (room lit from above) although they could not there get out : this was repeated many times. At the swarming time the bees were evidently positively heliotropic in special degree and the course of their emigration from the hive was determined by this factor. With the cover left off they altogether failed to get out.

It may be that the action of the immediate stimuli to migration in birds is susceptible of explanation on these lines. It has, indeed, already been supposed in this book that external agents may act on the birds when they are rendered sensitive to them by internal changes, and that this may result in emigratory departure. Migration might thus be said to resemble a negative tropism—negative, because the influential stimulus is in the conditions at the starting-point and not in those at the goal. But can the further course of migration be explained in any similar way ? The difficulty is to find any external agents in the physical order of things which could act to produce such complex but yet regular effects. One cannot assign very definite characters to the area of attraction : nor is the area the same for all birds or even for all individuals of one species. Nor is the course a direct one to that area, and the courses of different migrants may cross at right angles or even follow directly opposing courses. This absence of adequate external agents constitutes precisely the difficulty which makes it seem necessary to postulate racial memory, in a psychological sense, as a supplement to tropistic enregistrations.

Instinctive behaviour

Leaving aside these lower levels of conduct as inadequate, therefore, one has to consider migration as an example of instinctive behaviour. Here, however, one goes beyond the point up to which the biologist can give any satisfying explanation of the vital organisation involved, or can describe the relation between cause and effect in physiological to the exclusion of psychological terms.

The biologist cannot as yet explain the nature of instinctive behaviour, but he can describe what he means by the term. The general characteristics have been summarised by Lloyd Morgan as follows: "Instinctive behaviour is that which is, on its first occurrence, independent of prior experience; which tends to the well-being of the individual and the preservation of the race; which is similarly performed by all members of the same more or less restricted group of animals and which may be subject to subsequent modifications under the guidance of experience. Such behaviour is, I conceive, a more or less complex organic or biological response to a more or less complex group of stimuli of external and internal origin, and it is, as such, wholly dependent on how the organism, and especially the nervous system and brain centres, have been built up through heredity under that mode of racial preparation which we call biological evolution."

That this is a definition rather than an explanation must of course be granted, but it is to be observed that it is a general definition which aptly covers not only the particular case of bird-migration but also a very large number of similar activities of animals which are known to science. These examples, moreover, include many occurring at levels in the Animal Kingdom at which the possibility of any large admixture of intelligence may safely be ignored. They also include many cases in which the continuance of the custom as part of the germ-plasmic inheritance is easily demonstrated as against continuance by social tradition: one need only mention some of those complex sequences of behaviour exhibited at the very beginning of life by insects which emerge from the egg only after the death of the parent generation.

Beyond these general statements it is at present scarcely possible to go. "It is too soon," to quote J. Arthur Thomson, "to come to any hard-and-fast conclusion in regard

to the nature of instinctive behaviour. We have not yet got the facts fully before us, and there is much need of more experimental study. It is almost certain that there are different grades of instinctive behaviour. There are three main theories at present in the field. Some investigators rank instinctive behaviour as closely comparable to chains of reflex actions, and as due to non-cognitive hereditary dispositions to follow a certain routine when a number of stimuli present themselves. Others regard instinctive behaviour as quite inseparable from intelligent behaviour. According to a third view, instinct and intelligence are two radically different though often co-operative kinds of knowing, which have evolved along divergent lines."

As an exponent of this last view, Bergson has summed up the difference between instinct and intelligence in the following terms: "The intellect is characterised by a natural ability to comprehend life. Instinct on the contrary is moulded on the very form of life. While intelligence treats everything mechanically, instinct proceeds so to speak organically. If the consciousness that slumbers in it should awake, if it were wound up into knowledge, instead of being wound off into action, if we could ask and it could reply, it would give up to us the most intimate secrets of life."

Intelligent behaviour

It is in the main not necessary to seek higher than the level of instinctive behaviour in relation to bird-migration. Wholly intelligent behaviour could not account for conduct which must for many reasons be assumed to be the expression of an inborn mode of behaviour, which prepares for the unforeseen and secures "the evasion of a winter which will never be experienced," and which involves the traversing of a path of which the memory, apparently, must in the first instance often be in some degree racial and not individual. At the same time one need not neglect the possible admixture of intelligent to instinctive behaviour, the possible existence of some slight degree of awareness of the situation or even of some very dim consciousness of an end.

It should be noted, also, that in discussing whether behaviour is to be assigned to the plane of instinct or to that of intelligence one does not thereby intend to exclude the lower levels completely. On the contrary, action at

one of the higher levels necessarily includes many subordinate component acts of simpler kinds.

Migration problems in the light of the wider issues

The idea that behaviour must serve advantageous ends is covered by the biological concept of adaptation. Of this, migration certainly provides a remarkable example. The custom is an adaptation to the circumstances of the physical world in which the birds live, and dovetails into those other forms of behaviour, themselves adaptations, which are correlated with seasonal change. The adaptation has a survival value for its possessors in the struggle for existence.

The emergence of so complex and elaborate an adaptation is an example of the working of evolution, and as such raises many issues. Among these is the vexed question as to whether acquired habits can be inherited. The kindred question as to the inheritance of acquired morphological characteristics is still unsettled, and on this question itself there is as yet but little evidence. Pavlov is quoted by MacBride as having made experiments in training white mice to come for food when a bell was rung: it is stated that 300 lessons were required, but that the offspring of these trained mice learned in 100 lessons, the next generation in 30 lessons, and the next in 5 lessons. MacDowell, on the other hand, trained white rats to find their way to food in the centre of a maze, and found no improvement in the rate of learning in the offspring of trained parents, or in the offspring of trained parents and trained grandparents: other experiments have led to the same conclusion.

There is, however, no reason to go further into this question here. It is necessary only to note its existence and the consequent fact that in discussing theories as to the originating and developing causes of the migration custom one has to consider whether its beginnings are to be thought of as imposed upon all individuals by these causes and thereafter inherited, or as arising in some individuals as spontaneous variations in behaviour which survived in the process of natural selection.

Nevertheless, in view of the fact that no definite conclusion has been reached either about these causes or about the nature of the custom, it seems unprofitable, at present, to attempt any consideration of the possible manner in which the causes could have acted on the organism to produce the effect of an heritable line of behaviour. Nor need an

attempt be made here to pursue so general a question as the mode of inheritance ; let it be remarked, merely, that this problem of heredity is common to all cases of instinctive behaviour, and also that it cannot be escaped by explanations on tropistic or other mechanistic lines. The organism " trades with time," both in its individual life and in its racial history, and in its constitution there is somehow preserved the result of ages of experience.

When one comes to the question of the stimuli which periodically evoke migration one may seem to be on easier ground. A superficial explanation on simple mechanistic physiological lines is possible, as has been indicated, but there remains the deeper question as to how in the history of the race the particular stimulus and the particular response have become linked together as a natural chain of cause and effect.

Finally, when consideration is given to the factors which seem to determine the actual performance of the customary action, carrying it accurately through a complex sequence of phases in a more or less predetermined manner, one is driven back again upon the fundamental question of the nature of instinctive behaviour. It has been seen, indeed, that in the case of bird-migration in its most developed form it seems difficult to escape the conclusion that there is some racial memory of the path and goal of flight, and that this is inherited as an essential part of the racial custom : in less typical cases a tendency may be inherited in more general form, and the performance may be predetermined with less accuracy.

In general, it is obvious that to the question of the nature of instinctive behaviour all the other problems, in their wider implications, are subsidiary.

Conclusion

The general biological issues which are raised strike much deeper, and are much wider in their application, than the immediate problems of bird-migration with which this book has had to deal. In the relationship between the two sets of questions the ornithologist and the general biologist find common ground and each in the furtherance of his particular studies may assist the other. Thus to the ornithologist new light may come not only from increased knowledge of the facts of his own subject, but also from advances in the understanding of animal behaviour which

may open up new possibilities of explanation or remove existing difficulties. To the general biologist bird-migration offers an especially interesting example of instinctive behaviour, and in its further study he may hope to find new clues to the deeper secrets with which he is ultimately concerned. To study the migration of birds is to investigate the nature of animal behaviour, and to do this is to probe the inmost mysteries and to ask the very meaning of Life itself.

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APPENDIX

A NOTE ON SOME PRACTICAL BEARINGS OF THE STUDY OF BIRD-MIGRATION

Migration in relation to economic ornithology—International measures for bird protection—Birds and lighthouses—Birds as agents in the dispersal of plants and animals—Alleged transportation of disease infection.

In all the foregoing pages bird-migration has been considered solely as a subject studied for its interest to the naturalist and to the biologist. This final note, however, deals briefly with certain points which give the study importance from a utilitarian point of view. Although the points are only incidental to the objects of this book, it was felt that reference to them should not be altogether omitted. Principally, they arise from the relation of the facts of migration—theoretical considerations being here of secondary importance—to the other data of economic ornithology, and to practical measures for the conservation of bird-life.

The direct economic importance of wild birds is not very great. Only in small degree, in most countries, is mankind dependent upon their flesh and eggs as a source of food: in this country the value of sporting rights is of greater economic importance. The commerce in the plumage of wild birds for purposes of personal adornment, one is glad, is gradually coming to be looked upon, in civilised countries, as an illegitimate form of enterprise. Guano is important only in a few parts of the world.

The indirect economic importance of birds is enormous. Without them agriculture would be impossible, and all plant-life would be endangered by the rapid multiplication of insects and of small mammals. In this respect very many species of birds are to be classed as wholly beneficial, very many more as largely beneficial, and still others as at least neutral. Similar questions arise, but to a much less important extent, in relation to fisheries: some aquatic species feed on organisms harmful to the ova and fry of freshwater fishes, or on predatory species of fish, but others on the desirable fishes themselves, while in the sea some feed on fishes of no economic importance and others on those caught for human consumption—but it must not be rashly

assumed in any instance that the toll upon marine fishes is a serious one relatively to the enormous numbers which exist. Even in the few cases where a bird seems at first sight to be largely or wholly injurious to human material interests, it may play a part in the scheme of things which cannot be eliminated without disastrous results. The balance of nature, as many lessons have shown, is not to be disturbed with impunity, whether it be by the reduction or extinction of birds on the one hand or by excessive preferential protection, or by the artificial introduction of inappropriate species into new areas, on the other.

Unfortunately, these facts are not always understood, even among those who have most to gain from the knowledge. Thus, through prejudice, ignorance, and wantonness, through lust for destruction, greed for collection, and desire for gain, a great slaughter of birds goes on. To this must be added the indirect but immense effects of all the changes which civilisation works upon the face of the earth.

The economic reasons for increased and improved conservational measures become yearly greater and more urgent. This is not only the case in the older civilised countries, where the great growth of human populations and the increase in the deadliness of weapons have wrought enormous changes in recent times: the question is also already a pressing one in vast tracts of the newer countries where wild life was scarcely disturbed a few generations ago. To the utilitarian reasons are to be added every other—compassionate, æsthetic, or scientific—for desiring the protection of wild life.

In so far as protection is to be based on economic grounds, there is one point which makes migration a very relevant factor. The feeding habits of birds vary in some cases with the season of the year, either on account of differences in the available sources of food or in the kind of ground frequented, or on account of different needs. Thus, some birds which live largely on seeds feed their young on insects during the nestling period. Further, as has already been mentioned in this book, a given species may be represented in a particular area by individuals of which some are summer visitors, some winter visitors, and others resident throughout the year. A case can therefore be readily supposed where the summer visitant members of the species are to be assessed as largely beneficial, the resident members as, on balance, indifferent, and the winter visitant members as largely injurious. This is, of course, to take a purely local view of the situation, which is not greatly to be commended: a wider view would consider the facts in relation to the whole of the area inhabited by the species at any time of the year, and to the conditions in each part of it. The case will here suffice, however, to illustrate the necessity for taking seasonal movement into account in the study of economic ornithology.

Another point relevant to questions of protection arises from the constancy with which migratory birds return to the same

summer quarters. By reason of this the chances of a species becoming re-established when once it has been allowed to become extinct in a given breeding locality, are much diminished. If protection is given too late it may prove to be wholly useless. Recolonisation will be dependent on mere accident, unless the species survives in some immediately adjoining area or is one which is showing a definite tendency to extend its area owing, say, to over-population in more distant haunts. Even attempts at artificial reintroduction, if such be thought desirable, may be unsuccessful. Protection may therefore be too late if it be long delayed, even if the species holds its ground in other areas. This is an aspect of the subject which has obvious urgency where the breeding stock of a migratory species is becoming greatly depleted in any area.

Where protection is to be given at some seasons and not at others, a knowledge of the facts of migration will usually be of great importance. It may, for example, be desired specially to protect the small breeding stock of a species which is considered to be sufficiently abundant as a winter visitor to be a legitimate object of sport or of pot-hunting. The efficacy of protection during the breeding season must, in such a case, depend to some extent on what happens to the native birds during the winter: there may conceivably be times when the birds found along the coast are for the most part drawn from the inland breeding districts and not from the more spacious summer area in the far north. On the other hand, wild-fowlers have complained that a close-season in summer unnecessarily protects members of a species then lingering on our coasts and not due to breed in the far north until a much later date: one must admit that there is some logic in this, even although one would prefer that the birds should have the benefit of the circumstance.

Enough has been said to indicate the ways in which the facts of migration need to be taken into account in questions of economic ornithology and of bird-protection. The subject has received all too little attention from this point of view in most countries. The outstanding exception in Europe is Hungary, a country which depends largely on agriculture for its prosperity, and in which there has for long been a state-supported Institute of Ornithology attached to the Ministry of Agriculture. In the United States, also, economic ornithology was taken up by the Federal Government as long ago as 1885, and the task of investigation and public instruction entrusted to what is now the Biological Survey of the Department of Agriculture. It is noteworthy that both these services, in Hungary and in America, have paid particular attention to the subject of bird-migration, and have done so in a wide scientific spirit and not merely with a view to such utilitarian bearings of it as were immediately obvious.

The great lesson, however, to be learnt from the study of bird-migration in relation to bird-protection, is that measures

for the conservation of bird-life should be based upon international agreement and co-operation. The point is in reality so obvious that it need not be laboured, but the practical difficulties in the way of effective action are, in Europe, unfortunately very great. The insectivorous summer-visitant species in the British Isles enjoy for the most part a large degree of freedom from persecution, and this is based as much upon public feeling as upon legislation. But these same birds on their migrations, and in the winter quarters of some of them, are subject to wholesale slaughter in countries farther south. It is necessary not only that the area of protection should be as wide as possible, but also that the measures enforced in each part should be based on more than purely local considerations: it will not suffice that the breeding stocks in each country should be conserved there if they are to be destroyed elsewhere on the ground that the birds are only winter visitors.

The history of the movement in Europe for the international protection of birds has been recorded in detail by Herman, in an official publication of the Hungarian Ministry of Agriculture printed in the English language. The movement apparently originated from a resolution passed in 1868 at a congress of German agriculturists and foresters held in Vienna. The question was then taken up with other states by Austria-Hungary, resulting in a Declaration being signed in 1875 as between Austria and Hungary on the one hand and Italy on the other. Subsequently, certain other countries accepted the principle of the Declaration, but this was superseded by a Convention, signed in Paris in 1902, between the following states: Austria and Hungary, Germany, Belgium, Spain, France, Greece, Luxembourg, Monaco, Portugal, Sweden, and Switzerland.

A basis for agreement between many of the states of Europe does, then, exist; but it cannot be said that there is yet effective international action in the matter, or that all the contracting parties have in their own territories succeeded in enforcing the principles which they have formally accepted. Nor is it the case that countries outside the convention, including Great Britain and Holland, are by any means necessarily the most backward in their local legislative and executive efforts. The position, indeed, seems rather to be that the lamentable absence of public feeling on the subject in most South European countries continues to exercise an adverse effect upon the bird populations of the central and northern countries in which some attempt at rational conservation is now being made. Incidentally, it may be remarked that the most effectively protected birds in the British Isles, the common gallinaceous "game-birds," are practically non-migratory and therefore do not present the special problem here discussed.

(It has recently been stated in the press that Sweden is framing proposals for international agreement as to close seasons for birds of migratory species, and will approach Great Britain,

Holland, Belgium, Norway, Denmark, Finland, and Germany in this regard.)

The position in North America is much easier, owing to the fortunate circumstance that two countries, working in close accord in practical affairs, constitute the greater part of the continent. The underlying principles of the legislative position in the United States are of much interest in this connection. The State laws, varying from one state to another, are of primary importance and are based upon the assumption that all game and wild birds are the property of the state and may be killed only as the State Government may permit : landowners have no privileged position in this respect, except, of course, as regards access to their property. The Federal law before 1913 merely reinforced the local laws in incidental ways, *e.g.* as regards the taking of illegally killed birds from one state to another and as regards importation from abroad. In that year, however, it was decreed that birds which do not permanently remain within a given state are the property not of the state but of the United States Government, and so certain migratory species were protected by a Federal Act. (These facts are taken from a summary in the text-book of economic ornithology by Weed and Dearborn.)

The next logical step was to recognise that birds which do not permanently remain within the country as a whole cannot be even national property, and this principle seems to be implied, in effect at least, in the Migratory Bird Treaty signed in 1916, which provided for reciprocal legislation between Canada and the United States. This convention was implemented by the passage in Canada of the Migratory Birds' Convention Act, 1917, and in the United States of the Migratory Bird Treaty Act, 1918, the latter superseding the law of 1913, already mentioned. The treaty and the action taken by the parties to it are said to have already brought great benefit.

An incidental point with regard to the conservation of bird-life arises from the great destruction of migrants which takes place at lighthouses and lightships. Recently, the Royal Society for the Protection of Birds has arranged for the provision of bird-rests at a few of the lighthouses which are of most importance in this respect. The cost of these has been defrayed by voluntary subscription, but one hopes that in time the public conscience will have awakened sufficiently for these counteractive measures to become a duty of the authorities responsible for the lights. The provision of rests should save the lives of many thousands of birds which would otherwise perish by falling into the sea after being only slightly stunned, or by reason of exhaustion after fluttering for long in the glare.

This means will, of course, not avail to save those birds which are killed or seriously injured by forceful contact with the lantern glass. It is known, however, that coloured lights do not attract the birds as white ones so fatally do. It therefore

seems not unreasonable to ask that serious consideration should be given to the question of the gradual substitution of coloured for white lights at stations where great destruction commonly occurs and where the change may not be found to be impracticable for navigation reasons.

The final question to be considered here is that of the possible indirect effects of the movements of migratory birds. It is not to be doubted that birds can and at times do transport the seeds of plants, and also small organisms of the Animal Kingdom, from place to place. It is difficult to say whether or not birds, in their local movements, play an important part in this way in the economy of Nature. It is at least doubtful whether plants or animals are at all commonly transported by birds over the longer distances of migration flight. (Heintze has recently discussed the question with reference to the distribution of plants.)

The further suggestion has been made from time to time that wild birds may act as agents in transporting the micro-organisms of various infectious diseases of man and domestic animals, not only during local flights but even over greater distances on migration. No case of this kind is definitely known, but theoretically the possibility remains, and mention may therefore be made here of specific suggestions of the kind which have been put forward.

Not many years ago, for instance, some medical writers were of the opinion that diphtheria might be spread in this way. Thus, Sambon suggested in 1908 that winter epidemics of diphtheria in the eastern counties of England might owe their origin to the diphtheritic disease known to occur in the Wood-Pigeon (*Columba palumbus*), a species then abundant in the region owing to the influx of winter-visitors from the Continent. No evidence has been adduced showing any correlation between outbreaks of the human and avian diseases respectively, and this would now be scarcely worth seeking since it is known that avian diphtheria is an entirely distinct disease caused by a different organism. An epidemic which occurred among Wood-Pigeons in the autumn and winter, 1907–8, was investigated by Ticehurst. He found that the outbreak chiefly affected the counties bordering the Thames valley, and that it was apparently associated with massing of the birds, swollen in number by winter visitors, where there were exceptional crops of acorns or beech-mast. Some observers thought that the disease was found chiefly in the flocks of winter-visitant birds, but it would be very difficult to prove that the infection was brought from abroad. The disease was formerly believed to be caused by a diphtheroid bacillus often found associated with the condition, but it is now thought to be due to a more minute organism. Avian diphtheria, or "roup," is also found among domestic fowls and other birds, but it is apparently not known whether there is any correlation between outbreaks among poultry and epidemics in wild birds.

A more serious allegation against birds is that they may be

agents in the dissemination of foot-and-mouth disease among agricultural stock. This suggestion has been put forward at various times, by Mettam in 1915, for instance, and quite recently an agitation for the destruction of bird-life appears to have been made by farmers in a district of California which was overrun by the disease. This last case was officially investigated by Taylor and Bryant on behalf of the U.S. Department of Agriculture and the California Fish and Game Commission. They found no proof, either positive or negative, but thought that the theoretical arguments against the view preponderated. Even their suggestion that Turkey Buzzards might be shot when seen actually feeding on infected carcases, was made with an appearance of being a concession to popular feeling. It should be noted that in this case local spread rather than importation from a distance by migrants was the main point at issue.

Also quite recently, a definite suggestion has been made in this country by Stockman and Garnett that not only the local spread of foot-and-mouth disease but also its periodical introduction into the British Isles may be due to birds. They point out that the disease appears here during waves of prevalence on the Continent, in spite of all the preventive measures which are taken in respect of importation of animals and of straw and hay, and in spite of the fact that intervening periods occur in which the disease appears to have been completely stamped out. They proceed to argue that birds may be the means of bringing the infection from abroad, although there is no evidence either that birds contract the disease themselves or that the virus is viable in the conditions in which it could possibly be carried by this means.

While admitting the absence of any proof of the theory, these authors attempt to show that there is positive evidence in its favour. They claim to have discovered a remarkable relation between the seasonal and geographical incidence of initial outbreaks of the disease and the known immigratory movements of birds from the Continent. The matter is simplified by the fact that foot-and-mouth disease is rare in countries north of Denmark, and that the autumn and winter immigrations of birds from the north-east, north, and north-west may therefore be disregarded. The question thus resolves itself into that of a possible correlation between the introduction of the disease and (a) autumn and winter immigration and passage from the east on the southern portion of the east coast of England, and (b) spring and summer immigration and passage from the south. A correlation of this kind, the authors claim, is shown by a statistical examination of the dates and localities of initial outbreaks of disease.

The present writer (1924) has already criticised these arguments, questioned the validity of some of the data employed, and given a statement of his reasons for holding that the evidence produced by the authors does not warrant their conclusion. The figures given do not show any quantitative correspondence

between the numbers of initial outbreaks at different seasons and the magnitude of the appropriate bird movements. For instance, there is a relatively high figure for disease outbreaks in July, when migration is at its lowest ebb, and the figures for December and January are much higher than those for the months when the great autumn immigration is at its height. Again, the incidence of initial outbreaks remains low from March to June, while the main spring and summer immigration and passage movements from the south are taking place. As regards geographical incidence, it is perhaps possible to assign most of the apparent routes of disease invasion to the general directions of appropriate migration movements, but there is little indication of a quantitative relationship between the distribution of initial outbreaks and the importance of the different paths of bird-migration. For instance, it is claimed that the September, October, and November initial outbreaks occurred mainly in the part of England lying south of a line from the Bristol Channel to the Humber, the area chiefly affected by immigration at that season from the countries where the disease exists; but of 19 outbreaks in this area (as against 5 outside), only one was in Suffolk and none either in Norfolk or Essex, although on the coasts of these counties a very great part of this immigration from the east takes place. Again, during June, July, and August none of the 14 initial outbreaks occurred in an area of a dozen counties lying between the Wash and the Thames, although this region is one which is particularly affected by late summer passage to the north and which would be affected by any early autumn movement from the east. Taking the distribution of initial outbreaks as a whole, it indeed seems difficult to say more than that they occurred most frequently in the extreme south-east of England, the part nearest the Continent, and decreased in frequency westwards and northwards.

Although no case has been proved, or even established as probable, that any kind of disease of human beings or domesticated animals is commonly spread through the agency of birds, one must deprecate opposition to investigation of these questions based on a fear of resulting pleas for the removal of protection or even for the systematic destruction of birds. Proper inquiry is indeed more likely to put an end to agitation based on ignorance such as arose in the American instance just mentioned. In any event it should be quite obvious that even if the transport by birds of any form of disease infection should be proved, the remedy must lie in protective measures against the infection and not in any attempt at destruction of bird-life on a large scale. A destructive policy could not conceivably be carried out completely enough to achieve its object; the measure of its partial success would be the measure of the greater disasters in other directions which the loss of birds would lead to; and on every other ground it would be wholly unjustifiable.

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